
LEAF ARCHITECTURE OF THE CHLORANTHACEAE¹

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ABSTRACT

Leaves of 42 species of Chloranthaceae representing all four genera (*Sarcandra*, *Ascarina* (including *Ascarinopsis*), *Chloranthus*, and *Hedyosmum*) were cleared and examined to determine infrageneric and interfamilial relationships. Descriptions for all four genera are provided. Fifteen characters were examined, including: tooth type, secondary vein type, intramarginal vein, and leaf rank. Secondary architecture includes craspedodromous, semicraspedodromous, brochidodromous, and eucamptodromous patterns. Existing fossil evidence and proposals based on comparisons of extant genera are not sufficient to polarize these character states. The teeth in the Chloranthaceae are quite variable and three major types are characterized here. The leaf architecture of the Chloranthaceae is compared with that of the Lauraceae and Annonaceae, and, although the Chloranthaceae share a number of features in common with these two families, other characters suggest an ancient separation.

Although leaf architecture of extant angiosperms has been shown to be useful to identify fossil remains (Upchurch & Wolfe, 1987) and to elucidate intra- and interfamilial relationships (Levin, 1986a, b, c; Rury & Dickison, 1977), leaf architecture has been studied in only a relatively minute fraction of angiosperms. The leaf architecture of the Chloranthaceae is of particular interest because the position of the family in higher-order angiosperm classification is in dispute, and because some of the oldest known fossil floral parts (Friis et al., 1986) and fossil leaves (Upchurch, 1984a, b) are attributed to the Chloranthaceae. No in-depth studies have been conducted on the leaf architecture of the Chloranthaceae, and few critical studies have been conducted on leaf architecture in general. Especially few studies have been done in the Magnoliidae (Doyle & Hickey, 1976; Hickey & Wolfe, 1975; Klucking, 1986, 1987).

The Chloranthaceae are a small pantropical family with four genera and approximately 70 species. The four genera fall into two distinct groups. *Sarcandra* and *Chloranthus* are distinguished by bisexual flowers and an herbaceous or suffrutescent habit; they are confined to Indomalasia (Verdcourt, 1986). *Ascarina* and *Hedyosmum*, on the other hand, are distinguished by their unisexual flowers and arborescent or shrubby habit. *Ascarina* ranges

from New Zealand to New Caledonia and Malesia with one disjunct species (originally placed in its own genus, *Ascarinopsis*) in Madagascar (Jeremie, 1980; Swamy, 1953; Verdcourt, 1985, 1986). *Hedyosmum* occurs from Mexico to Brazil and the West Indies with one disjunct species in Southeast Asia (Todzia, 1988).

Some authors have suggested that the Chloranthaceae are among the most primitive families of angiosperms and at the root of the Hamamelid and Magnoliid lines (Burger, 1977; Endress, 1987). The fossil record of the family and closely related forms dates to the Early Cretaceous and includes pollen (see Walker & Walker, 1984, for summary), leaves (Upchurch, 1984a, b), and flowers (Crane et al., 1989; Friis et al., 1986) (see Crane, 1989, for review). The Chloranthaceae also have been postulated to have an important position in the separation of the monocot and dicot phylogenetic lineages (Burger, 1977).

Furthermore, much controversy surrounds the placement of the Chloranthaceae in higher-order angiosperm classification (see Verdcourt, 1985). In recent classifications the family has been placed in the Piperales (Cronquist, 1981), Magnoliales (Dahlgren, 1980), Laurales (Takhtajan, 1980), and the Annonales (Thorne, 1976). Recent studies of floral anatomy strongly suggest placement of the

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Chloranthaceae in the Laurales near the Trimeniaceae and Amborellaceae (Endress, 1986, 1987; Endress & Sampson, 1983). Endress (1987) suggested that the family may link the Laurales and the Piperales as well as being pivotal to understanding the separation of the Hamamelidae and the Magnoliidae.

The present study was undertaken to examine the leaf architecture of the Chloranthaceae in order to provide additional information for generic circumscription and to shed new light on intrafamilial and interfamilial relationships of the family. The specific objectives of this investigation are (1) to provide a comprehensive description of the leaf architecture of the Chloranthaceae; (2) to outline basic trends of specialization in the architecture of chloranthaceous leaves; (3) to look at the relationship of leaf architecture and elevation in *Hedyosmum* species; and (4) to provide leaf architectural data that will contribute to a better understanding of the interfamilial relationships of the family.

MATERIALS AND METHODS

Leaves of 45 species of Chloranthaceae representing all four genera were studied (Table 1). The most completely surveyed genus was *Hedyosmum* in which leaves of 37 of the 40 species were cleared. Leaf clearings were done following Fuchs's Method No. 1 (Fuchs, 1963) with some modification. Leaves were obtained from FAA-preserved material or dried herbarium specimens, placed in 80% ETOH for several days, and then slowly rehydrated. The specimens were subsequently placed in a solution of 1% basic fuchsin in 10% sodium hydroxide for 12–36 hours in a 60°C oven and then washed in water for several days. After dehydration, the leaves were immersed in a mixture of 3 parts absolute alcohol and 1 part concentrated HCl and then washed in absolute alcohol for 48 hours. After two xylene rinses, the specimens were mounted on slides with permount.

Leaves with thick waxy cuticles that prevented infiltration of the NaOH-basic fuchsin solution were pretreated with 100% dichloromethane. After 0.5–2.0 hours in dichloromethane, the leaves were washed in absolute alcohol before the dehydration series. Leaves with large amounts of tannin deposits that obscured the internal features were pretreated with 10% ammonium hydroxide for 1–5 minutes and then rinsed well before continuing the basic fuchsin-sodium hydroxide procedure.

Many of the principal character states and discrete features are summarized in Table 2. The only comprehensive sample here is *Hedyosmum*. One

of the two species of *Sarcandra* is represented. Only small representations of *Ascarina* and *Chloranthus* are given. Five out of 20 species of *Chloranthus* and three out of 11 species of *Ascarina* were sampled.

CHARACTERS

Leaf architectural terminology generally follows Hickey (1973, 1977, 1979). Fifteen characters were examined (Table 2), the following of which require more explanation.

(8) Tooth type. The six different variants found in the Chloranthaceae were given the following codes: 1A, 1B, 2A, 2B, 2C, and 3. A detailed description of each type is provided in the discussion section.

(9) Secondary vein type. In addition to the standard brochidodromous arrangement where some secondaries are joined in a series of prominent arches, some leaves have the secondaries upturned and gradually diminishing apically inside the margin and thus are intermediate between brochidodromy and eucamptodromy. The condition where the secondary veins are not looped near the apex is designated EB, and the less common case when the unlooped secondary veins are near the base is called BE. The semicraspedodromous (S) condition may occur when secondary loops branch sending the admedial branch to join the superadjacent secondary vein and the exmedial branch to a tooth. This is seen in *Chloranthus* (Fig. 5), *Hedyosmum* (Figs. 11, 14), and *Sarcandra* (Fig. 2). A less well organized version is like the above but with some branches from secondary arches forming tertiary and higher order loops and other branches entering teeth. Upchurch (pers. comm.) calls this "festooned craspedodromous" (FC), and this can be seen in *Ascarina* (Figs. 3, 6).

(11) Presence of an intramarginal vein. This refers to a collector vein formed from the loops of the secondary veins and is usually present within 2–4 mm of the leaf margin.

(12) Presence of an intermarginal vein or fimbrial vein. This refers to the vein immediately within the leaf margin. Tertiary veins usually unite to form the fimbrial vein.

(13) Highest vein order. Leaf veins branch repeatedly, producing higher orders of venation. The primary vein (or midvein) of the leaf is the first rank with the second rank composed of secondaries or the major lateral veins. The next finer set arising from both primary and secondary veins is designated the tertiary veins and so on, until the

TABLE 1. Collection data for specimens used in Chloranthaceae leaf architecture study.

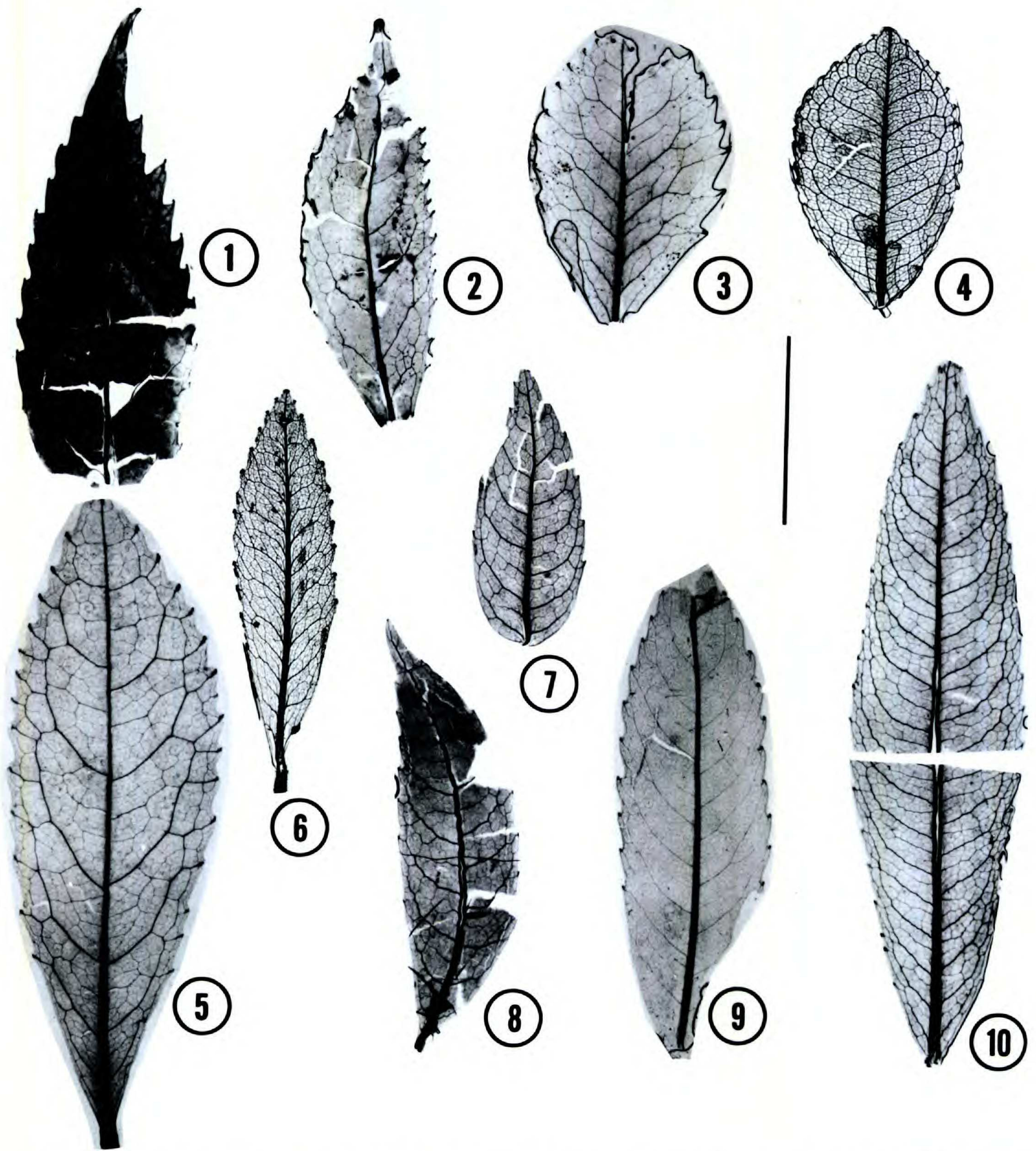
Species	Collection	Country	State or province	Elevation
<i>Sarcandra</i>				
<i>S. glabra</i> (Thunb.) Nakai subsp. <i>glabra</i>	Wood et al. 3849 A, MO	Taiwan	Taipei Hsien	N/A
<i>S. glabra</i> subsp. <i>brachystachys</i> (Blume) Verdcourt	Levine 3170 MO	China	Guangxi	N/A
<i>Chloranthus</i>				
<i>C. erectus</i> (Buch.-Ham.) Verdcourt	J. Sinclair 6553 US	N/A	N/A	N/A
<i>C. angustifolius</i> Oliver	Henry 658 GH	China	N/A	N/A
<i>C. spicatus</i> Pei	C. O. Levine 693 A	N/A	N/A	N/A
<i>Ascarina</i>				
<i>A. lucida</i> Hook.f.	Melville 6878 A	New Zealand	Westland	N/A
<i>A. philippinensis</i> C. B. Rob.	Schodde 4897 US	New Guinea	N/A	N/A
<i>A. rubricaulis</i> Solms-Laub.	McPherson 6486 MO	New Caledonia	Mt. Do	N/A
<i>Hedyosmum</i> subg. <i>Hedyosmum</i> sect. <i>Orientalis</i>				
<i>Hedyosmum orientale</i> Merrill & Chun	Tsang 26692 A	China	Kwangtung	N/A
<i>Hedyosmum grisebachii</i> Solms-Laub.	Alain et al. 5523 GH, US	Cuba	Oriente	N/A
<i>Hedyosmum domingense</i> Urban	Morton 9338 US	Cuba	Oriente	1,600–1,800 m
<i>Hedyosmum subintegrum</i> Urban	Shafer 8061 NY, US	Cuba	Oriente	N/A
<i>Hedyosmum</i> subg. <i>Hedyosmum</i> sect. <i>Hedyosmum</i>				
<i>Hedyosmum nutans</i> Sw.	Morley et al. 937 A, B, MO, S	Jamaica	Clarendon	975 m
<i>Hedyosmum brenesii</i> Standley	Grayum et al. 3550 MO, TEX	Costa Rica	Limón	ca. 400 m
<i>Hedyosmum</i> subg. <i>Tafalla</i> sect. <i>Microcarpa</i>				
<i>Hedyosmum pseudoandromeda</i> Solms-Laub.	Steyermark 91,705 F, GH, NY, US	Venezuela	Distrito Federal	2,300 m
<i>Hedyosmum gentryi</i> D'Arcy & Liesner	Plowman 13,396 F, TEX	Venezuela	Fálcon	1,200–1,400 m
<i>Hedyosmum neblinae</i> Todzia	Gentry & Stein 46700 MO, TEX	Venezuela	Amazonas	1,900–2,100 m
<i>Hedyosmum arborescens</i> Sw	Anderson 3257 DUKE, LL, GH, US	Jamaica	Portland	1,310–1,371 m
<i>Hedyosmum costaricense</i> W. Burger	Todzia 2038 CR, TEX	Costa Rica	San José	1,100 m
<i>Hedyosmum burgerianum</i> D'Arcy & Liesner	Todzia & Schmalzel 2578 MO, TEX	Panama	Chiriquí	1,500–1,600 m
<i>Hedyosmum bonplandianum</i> HBK	Todzia 2545 F, GH, MO, NY, TEX, US	Panama	Chiriquí	900–1,100 m
<i>Hedyosmum racemosum</i> (Ruiz Lopez & Pavón) G. Don	Todzia & Grimes 2516 AAU, MO, NY, QCA, QCNE, TEX, US	Ecuador	Zamora-Chinchi	2,500 m

TABLE 1. Continued.

Species	Collection	Country	State or province	Elevation
<i>Hedyosmum sprucei</i> Solms-Laub.	Todzia & Grimes 2520 QCA, QCNE, TEX	Ecuador	Pastaza	900-1,000 m
<i>Hedyosmum brasiliense</i> Mart. ex Miq.	Todzia & Hatschbach 2384 AAU, CAS, F, G, GH, F, MO, NY, S, TEX, US	Brazil	Paraná	10-25 m
<i>Hedyosmum goudotianum</i> Solms-Laub.	Todzia 2391 F, GH, MO, NY, TEX, US	Colombia	Antioquia	ca. 2,500 m
<i>Hedyosmum correanum</i> D'Arcy & Liesner	Todzia 2550 F, GH, MO, NY, TEX, US	Panama	Chiriquí	1,500-1,600 m
<i>Hedyosmum colombianum</i> Cuatrecasas	Todzia 2425 COL, F, JAUM, MO, NY, TEX	Colombia	Cundinamarca	ca. 2,500 m
<i>Hedyosmum crenatum</i> Occhioni	Todzia 2430 COL, F, HUA, JAUM, MO, NY, TEX, US	Colombia	Cundinamarca	ca. 3,100 m
<i>Hedyosmum strigosum</i> Todzia	Todzia & Grimes 2530 MO, TEX, QCA, QCNE	Ecuador	Napo	2,530 m
<i>Hedyosmum anisodorum</i> Todzia	Todzia & Grimes 2475 F, MO, NY, QCA, QCNE, TEX	Ecuador	Pichincha	2,000-2,500 m
<i>Hedyosmum steinii</i> Todzia	Lozano 3165 COL	Colombia	Chocó	1,700-1,950 m
<i>Hedyosmum spectabile</i> Todzia	Todzia & Grimes 2515 MO, NY, QCA, QCNE, TEX	Ecuador	Zamora-Chinchipe	2,500 m
<i>Hedyosmum scaberrimum</i> Standley	Todzia 2539 MO, TEX	Panama	Coclé	780-900 m
<i>Hedyosmum translucidum</i> Cuatrecasas	Todzia 2417 AAU, COL, JAUM, MO, NY, PSO, TEX	Colombia	Putumayo	2,600-2,800 m
<i>Hedyosmum dombeyanum</i> Solms-Laub.	Todzia & Stein 2699 F, GH, NY, MO, TEX, US, USM	Peru	San Martín	1,900-1,950 m
<i>Hedyosmum lechleri</i> Solms-Laub.	Todzia & Stein 2733 F, MO, TEX, USM	Peru	Huánuco	2,400 m

TABLE 1. Continued.

Species	Collection	Country	State or province	Elevation
Hedyosmum subg. Tafalla sect. Artocarpoides <i>Hedyosmum mexicanum</i> Cordemoy	<i>Todzia & Schmalzel 2580</i> MO, TEX	Panama	Chiriquí	1,800 m
Hedyosmum subg. Tafalla sect. Macrocarpa <i>Hedyosmum scabrum</i> (Ruiz Lopez & Pavón) Solms-Laub	<i>Todzia & Grimes 2514</i> F, MO, NY, QCA, QCNE	Ecuador	Loja	2,700 m
<i>Hedyosmum angustifolium</i> (Ruiz Lopez & Pavón) Solms-Laub	<i>Todzia & Stein 2764</i> TEX, USM	Peru	Junín	1,300–1,400 m
<i>Hedyosmum maximum</i> (Kuntze) K. Schumann	Steinbach 591 GH, MO, NY, US	Bolivia	Cochabamba	3,450 m
<i>Hedyosmum cumbalense</i> Karsten	<i>Todzia & Grimes 2492</i> MO, QCA, TEX	Ecuador	Carchi	3,200–3,300 m
<i>Hedyosmum parvifolium</i> Solms-Laub.	Luteyn 5331 AAU, COL, MO, NY, US	Venezuela	Táchira	2,500–3,200 m
<i>Hedyosmum cuatrecazanum</i> Oechioni	<i>Todzia & Grimes 2505</i> F, MO, NY, QCA, QCNE, TEX, US	Ecuador	Azuay	2,600–2,800 m
<i>Hedyosmum luteynii</i> Todzia	<i>Todzia & Grimes 2480</i> MO, NY, QCA, QCNE, TEX, US	Ecuador	Napo	3,000–3,100 m
<i>Hedyosmum peruvianum</i> Todzia	<i>Todzia & Stein 2731</i> AAU, F, GH, K, MO, NY, TEX, USM	Peru	Huánuco	2,400–2,600 m



FIGURES 1-10. Cleared leaves of *Sarcandra*, *Ascarina*, *Chloranthus*, and *Hedyosmum*.—1. *Sarcandra glabra* subsp. *brachystachys*.—2. *Sarcandra glabra* subsp. *glabra*.—3. *Ascarina lucida*.—4. *Ascarina philippinensis*.—5. *Chloranthus spicatus*.—6. *Ascarina rubricaulis*.—7. *Hedyosmum domingense*.—8. *Hedyosmum subintegrum*.—9. *Hedyosmum nutans*.—10. *Hedyosmum grisebachii*. Scale line = 2 cm.

ultimate vein order present in the leaf is reached (Hickey, 1973).

(15) Number of free endings/areole. The actual range of the number of freely ending veinlets within an areole is reported. Although several degrees of branching are usually present within a single leaf, range of the degree of veinlet branching appears to be consistent within a species.

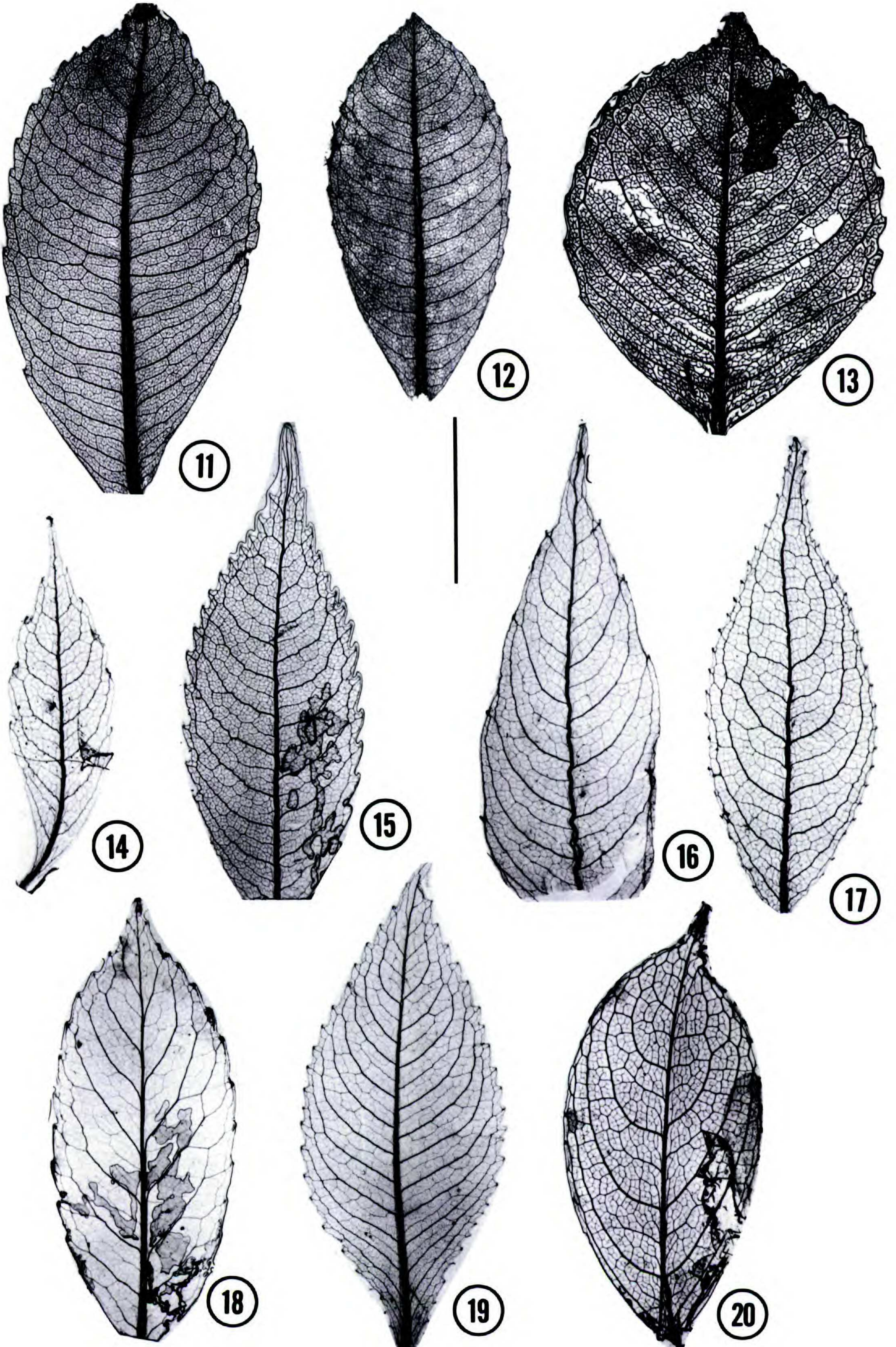
(16) Leaf rank. According to Hickey (1977, p. 158), leaf venation is organized into four levels or ranks. Leaf rank is based primarily on the highest vein order in which the veins follow a regular course and delimit areas of relatively consistent size and shape. First rank leaves have secondary and higher order veins following an irregular course. The intercostal areas are irregular in shape, as are

TABLE 2. Leaf architecture data. (1) In *Hedyosmum* the sectional alignments are given as follows: * subg. *Hedyosmum* sect. *Orientele*; \diamond subg. *Hedyosmum* sect. *Hedyosmum*; + subg. *Tafalla* sect. *Microcarpa*; ! subg. *Tafalla* sect. *Microcarpa*; ● subg. *Tafalla* sect. *Macrocarpa*. (2) & (3) Data representative for species, not just individual cleared leaves. (4) Leaf shape: el = elliptic, la = lanceolate, li = linear, n = narrowly, ob = obovate, ov = ovate, w = widely. (5) Average leaf length/width ratio. (6) Leaf apex: acm = acuminate, act = acute, b = broadly, l = long, ob = obtuse. (7) Leaf base: cun = cuneate, n = narrowly, obt = obtuse, rd = rounded, trun = truncate. (8) Tooth type: see text for discussion. (9) Secondary vein type: B = brochidodromous, S = semicraspedodromous, E = eucamptodromous, FC = festooned craspedodromous. (10) Average number of major secondary veins per leaf side. (11) Presence or absence of an intramarginal vein. (12) Presence or absence of an intermarginal (or fimbrial) vein. (13) Highest vein order. (14) Areole size. 1 = very large >2 mm, 2 = large 2–1 mm, 3 = medium 1–0.3 mm, 4 = small <0.3 mm. (15) Number of free vein endings/areole. (16) Leaf rank explained in text.

(1) Species	(2) Length (cm)	(3) Width (cm)	(4) (Shape)	(5) l/w ratio	(6) Apex
<i>S. glabra</i> subsp. <i>glabra</i>	2–20	1–8	la to el	2.4:1	l-acm
<i>S. glabra</i> subsp. <i>brachystachys</i>	2–20	1–8	la to el		l-acm
<i>C. erectus</i>	8–29*	3–13*	el	5:1	acm
<i>A. lucida</i>	2–7	2–4	el, ov	1.5:1	act
<i>A. philippinensis</i>	3–14(–18)	2–8(–10)	el, ob, ov	1.7:1	ob, acm
<i>A. rubricaulis</i>	5–12	1–3	la	4.2:1	acm
* <i>H. orientale</i>	(9–)15–25	1–3	la to li-ob	10:1	l-acm
* <i>H. grisebachii</i>	7–13	2–3	la to ob-la	4:1	l-acm
* <i>H. domingense</i>	4–6(–8)	1–2	la to n el	3.3:1	acm
* <i>H. subintegrum</i>	(2–)5–8	1–2	n el, n ob	4.3:1	acm
\diamond <i>H. nutans</i>	5–14	1–2	la	6.3:1	acm
\diamond <i>H. brenesii</i>	6–16	1–4	li-la, n el	4.4:1	l-acm
+ <i>H. pseudoandromeda</i>	3–4(–6)	2–3	el, n el	1.4:1	act
+ <i>H. gentryi</i>	6–16	3–6	ob to el	2.4:1	acm
+ <i>H. neblinae</i>	(4–)6–9	3–6	ov to w el	1.7:1	act, acm
+ <i>H. arborescens</i>	(3–)5–12(–18)	2–6	el	2.1:1	l-acm
+ <i>H. costaricense</i>	(4–)8–15(–20)	2–5(–7)	n el, el	3.3:1	l-acm
+ <i>H. burgerianum</i>	3–6	1–2	ov to ob	3:1	l-acm
+ <i>H. bonplandianum</i>	5–13(–17)	(2–)4–7	n el, el, ov	1.6:1	acm
+ <i>H. racemosum</i>	6–23	3–8	ob, el, ov	2.6:1	acm
+ <i>H. sprucei</i>	(5–)8–19(–22)	(2–)4–8	n el, n ob	2.2:1	acm
+ <i>H. brasiliense</i>	8–21	2–6(7)	n ov, n ob	3.6:1	acm
+ <i>H. goudotianum</i>	(3–)6–16(–19)	2–7(–8)	n el, ov, ob	2.4:1	acm
+ <i>H. correanum</i>	(3–)5–9	1–4	ov, ob, el	2.8:1	acm
+ <i>H. colombianum</i>	6–15(–18)	2–7	el, ob	2.5:1	acm
+ <i>H. crenatum</i>	(4–)5–11(–14)	2–4(–5)	n el, el	3:1	acm
+ <i>H. strigosum</i>	8–17(–21)	3–8	el to n el	2.1:1	acm
+ <i>H. anisodorum</i>	(9–)14–22(–29)	5–8(–10)	n el, n ob	2.8:1	acm
+ <i>H. steinii</i>	4–12	2–5	n el, el	2.3:1	acm
+ <i>H. spectabile</i>	(6–)10–20	(3–)5–8	el, ov	2.3:1	acm
+ <i>H. scaberrimum</i>	(5)8–27	3–6(–8)	el, n el	3.9:1	acm
+ <i>H. translucidum</i>	5–12(–16)	2–4(–5)	n ob, n el	2.4:1	acm
+ <i>H. dombeyanum</i>	5–10	2–5	n el, ob	2.1:1	acm
+ <i>H. lechleri</i>	4–12	2–4	n el, el	2.7:1	acm
! <i>H. mexicanum</i>	10–25	2–7	la, ob-la	3.9:1	l-acm
● <i>H. scabrum</i>	6–13(–16)	2–7	n el, el, ob	2.1:1	acm
● <i>H. angustifolium</i>	(5–)12–17	2–5	la, el, ob-la	4.1:1	acm
● <i>H. maximum</i>	8–14	4–6	el	2.2:1	acm
● <i>H. cumbalense</i>	1–5	0.5–2	n el, el, ob	2.4:1	acm
● <i>H. parvifolium</i>	(2–)4–9	2–3	n el, el, ob	2.6:1	act, acm
● <i>H. cuatrecazanum</i>	(5–)8–19	2–8	ob, n ob, n el	2.7:1	acm
● <i>H. luteynii</i>	4–8(–13)	3–5(–8)	ob, el	1.5:1	acm
● <i>H. peruvianum</i>	(8–)12–22	(3–)5–9	n el, el	2.4:1	acm

TABLE 2. Continued.

(7) Base	(8) Tooth type	(9) 2° vein type	(10) 2° vein no.	(11) Intra mar. vein	(12) Inter mar. vein	(13) Highest vein	(14) Areole size	(15) No. vein end- ings	(16) Leaf rank
cun	2B	S	4-5	-	+	5	2	1-5	2r ⁰
cun	2B, 2C	EB	8	-	-	5	2	0-2	1r ¹
cun	2B	EB, S	6-9	-	-	6	3	0-2	—
cun	3	FC	7	-	-	4-5	2	0-5	2r ⁰
cun	2A	EB	9	-	±	5	2-3	0-2	2r ¹
cun	2A	FC	10	-	-	5	2-3	0-4	2r ¹
n cun	2B	EB	18	-	-	4-5	2	0-1	2r ⁰
cun	1, 2A	EB	16	+	+	5	2	0-3	2r ¹
rd	2A	B	7	-	+	5	2	2-4	2r ³
cun	1	BE	8	-	+	5	3	2-3	2r ¹
rd, cun	1, 2A	S	10	-	+	5	2	0-3	2r ²
cun	2B	E	15	-	+	5	2-3	0-2	2r ¹
obt, cun	2A	B	14	+	+	5	3	0-2	2r ²
b cun	2A	EB	12	+	+	5	2	1-3	2r ³
obt, trun	2A	EB	11	+	+	5	1	0-2	2r ³
cun, obt cun	2B	EB, S	13	+	+	5	2	0-2	3r ⁰
rd, b cun	2A	E	9	+	+	5	2	0-2	2r ²
cun	2A, 2B	EB	8	±	±	5	2	0-2	2r ²
cun, obt cun	2B	E	8	-	-	5	2	0-3	2r ¹
cun, obt cun	1B	E	5-12	-	±	5	2	0-3	3r ¹
cun, obt cun	1	E	11	-	-	5	3	0-3	3r ¹
cun, obt cun	1B, 2A	EB	8	-	-	5	2	0-3	2r ⁰
cun, obt cun	3	E or B	8	-	-	5	2	2-3	4r ⁰
cun	3	E	7	-	-	5	2	0-2	2r ¹
cun	2A	E	11	-	-	5	2-3	0-2	2r ¹
cun, obt cun	1B, 2A	E	6	-	-	5	2	0-2	3r ⁰
rd, obt rd	1A	E	N/A	-	-	5	2	0-2	3r ⁰
n cun	3	E	9	-	±	5	2	0-2	2r ¹
cun, obt cun	3	E	7	+	-	5	2	0-2	2r ¹
cun, rd	3	E	6	-	-	5-7	2	0-6	4r ⁰
cun, obt cun	3	E	6-12	-	-	5	2	0-2	2r ¹
cun, obt cun	3	E	10-12	-	-	5	2	0-3	2r ³
cun	2A	E	8-10	+	-	5	2	0-2	2r ¹
obt, cun	1B	EB	9	+	-	5	2	0-2	2r ¹
cun, obt cun	1A, 1B, 2A	E	12-14	-	-	5	2	0-3	2r ³
cun	1A	B	20	±	±	5	2	0-1	3r ³
cun, obt cun	1B	EB	15	-	-	5	2	0-2	2r ³
b cun, obt cun	1A	EB	10	-	-	5-6	2-3	0-4	2r ²
rd, trun	1B	EB	13	±	±	5	2	0-2	2r ³
cun, obt	2A	E	16	-	-	5	2	0-2	2r ³
cun, ob cun	1B	EB	14	-	±	5	2-3	0-2	3r ⁰
n-b-obt cun	1A	B	16	-	±	5	2	0-2	3r ⁰
cun, obt cun	1B	E	18	-	±	5	3	0-2	3r ¹



the tertiary and quaternary domains. Domains are areas delimited by veins of tertiary and higher rank. Second rank leaves have regularly shaped intercostal areas, but higher domains are not uniform in size or shape. Third rank leaves have relatively consistent (predictable) tertiary domains. Fourth rank leaves have areoles of predictable or uniform size and shape.

Within each of the main ranks, subranks 0–3 are recognized based on the degree of advancement (increasing regularity of pattern) toward the next level. The assignment of subranks would be based on the assessment of the status of the following kinds of morphoclines. Secondary and higher order veins may arise from the next lower level at decurrent, acute, orthogonal, or obtuse angles. Vein endings within areoles may be a high number, a low number, rare, or absent. In a brochidodromous leaf there may be several orders of loops, few loops (festooned), no loops, and finally, the straightening of the arches into an intramarginal vein. In each of these sequences, one would assign a low subrank (0–1) for the beginning of the morphocline and high subrank (2–3) at the other end of the morphocline. These sequences are read in a direction of increasing specialization as supported by analyses of fossil floras. Leaves with low rank appear first in the fossil record, and it seems that leaf venation rank order correlates with the degree of advancement of the whole plant as determined by other evidence (Doyle & Hickey, 1976; Hickey, 1977; Hickey & Wolfe, 1975; Thomas & Spicer, 1987).

Leaf length and width were plotted in scatter diagrams using log scales. Samples of up to ten specimens were used for each species, if available.

GENERIC DESCRIPTIONS

SARCANDRA GARDNER (FIGS. 1, 2, 45, 46)

Leaves elliptic, chartaceous, with length/width ratios of 3–4:1. The apex acuminate and the base cuneate to decurrent. Margin usually boldly toothed with deeper sinuses than the other genera. Sinuses rounded. The median vein to the tooth apex arising from secondaries. Petiole very short with a decurrent wing of laminar tissue on petiole. Secondary venation either semicraspedodromous or brochidodromous with basal secondary veins forming loops

but tending toward eucamptodromy. Secondary veins alternate, widely spaced with about five per side, arising at an acute angle and curving apically. Intercostal areas large and irregular. Intersecondaries, about two per intercostal area, mostly simple but sometimes composite. Tertiary veins acute admedially and exmedially. Tertiary and quaternary domains both random polygonal. Highest vein resolution five. Areole development imperfect, arrangement random, and irregularly shaped. Areoles 1–2 mm with 0–5 veinlets per areole. Druses random or absent. Stone cells present in loose clusters near the midvein.

CHLORANTHUS SW. (FIG. 5)

Leaves 4–30 cm long, elliptic, with length/width ratios of 3–5:1. The apex acuminate and the base cuneate to decurrent. Margin serrate with teeth closely adjacent to the shallow, rounded sinus. Basal side of tooth slightly convex. The tooth hydathodal with one or more large stomates on the tooth surface distal to the dilated median vein of the tooth. Leaf texture chartaceous and the petiole very short with a decurrent wing of laminar tissue. Secondary venation brochidodromous with a broad row of marginal loops or distally brochidodromous and proximally eucamptodromous with marginal loops that produce tooth veins. Secondary veins acute, usually widely spaced, with 6–9 per side of the midvein, alternate or subopposite. Intercostal areas irregular and gradually apically curving. Intersecondaries common, 1–2 per intercostal area, and ranging from simple or composite. Tertiary and quaternary domains irregularly polygonal in size and shape. Highest vein resolution five. The imperfectly developed areoles polygonal and randomly arranged, and about 0.5–2.5 mm long. Stomates common and randomly arranged over the abaxial epidermis. Prismatic crystals occurring singly or in clusters and randomly distributed in the lamina, often in and near teeth but also closer to the midvein. The clusters not like druses but appearing eroded.

ASCARINA J. R. & G. FORST. (FIGS. 3, 4, 6)

Leaves elliptic, with length/width ratios of 1.5–4.2:1. The apex acuminate to obtuse and the base cuneate. Margins serrate with the tooth apex close

←

FIGURES 11–20. Leaf clearings of *Hedyosmum*.—11. *H. gentryi*.—12. *H. pseudoandromeda*.—13. *H. neblinae*.—14. *H. burgerianum*.—15. *H. arborescens*.—16. *H. costaricense*.—17. *H. racemosum*.—18. *H. brasiliense*.—19. *H. mexicanum*.—20. *H. bonplandianum*. Scale line = 2 cm.

to the sinus. The sinus rounded. Leaf texture chartaceous to coriaceous. Petiole very short, with a decurrent wing of laminar tissue. Secondary venation a combination of festooned brochidodromous and semicraspedodromous, the secondary veins forming a series of loops near the margin and branches of looping secondary veins enter the teeth. *Ascarina philippinensis* with regular brochidodromous arches. *Ascarina rubricaulis* with strongly decurrent intersecondary veins arising either from the midvein or from a secondary vein. Other *Ascarina* species with \pm nondecurrent intersecondary veins that arise only from the midvein, as in *Sarcandra* and *Chloranthus*. The 6–8 secondary veins producing somewhat regular to very regular intercostal areas. A few simple or composite intersecondary veins present. Tertiary and quaternary veins forming irregular and polygonal domains. Highest vein order 4–5. The randomly arranged areoles imperfect and irregular to polygonal. Areoles 0.3–1 mm and showing strong tendency to be elongate and parallel to the secondary veins or at right angle to the midvein. Crystals absent. Stone cells free or clustered near the midvein, or in short rows along the midvein.

HEDYOSMUM SW. (FIGS. 7–44, 47, 48, 49)

Leaves ovate to oblanceolate, elliptic, obovate varying in size from 1 to 29 cm, with length/width ratios of 1.5–10:1. The apex mostly acuminate to occasionally obtuse and the base mostly cuneate to truncate or obtuse. Margin serrate with various forms of glandular teeth. Most teeth convex basally with a small, rounded sinus. The tooth apex often close to the sinus. Texture chartaceous to coriaceous. The petiole very short with a decurrent wing of laminar tissue. Secondary venation brochidodromous, eucamptodromous, or transitional, and occasionally looped. Venation occasionally semicraspedodromous. Brochidodromous arches occasionally aligned forming an intramarginal vein. Secondaries often more numerous than 12–15 per side, acute and curving apically. Intercostal areas often very

regular. Intersecondaries absent or present as simple or composite. Tertiary and quaternary veins usually irregular and polygonal. Highest vein order present usually 5 (rarely to 7). Areole development imperfect to well developed in about 20% of the species. Areole shape polygonal to irregular, usually randomly oriented. Size quite variable within a specimen and varies for the genus between 0.3 and 2.0 mm. Veinlets varying from 0–1 to 2–4 or 0–6 per areole and sometimes branched several times. Crystals absent. Sclerenchyma varied, stone cells, single or clustered, branched spongy mesophyll cells and branched vein sheath cells.

DISCUSSION

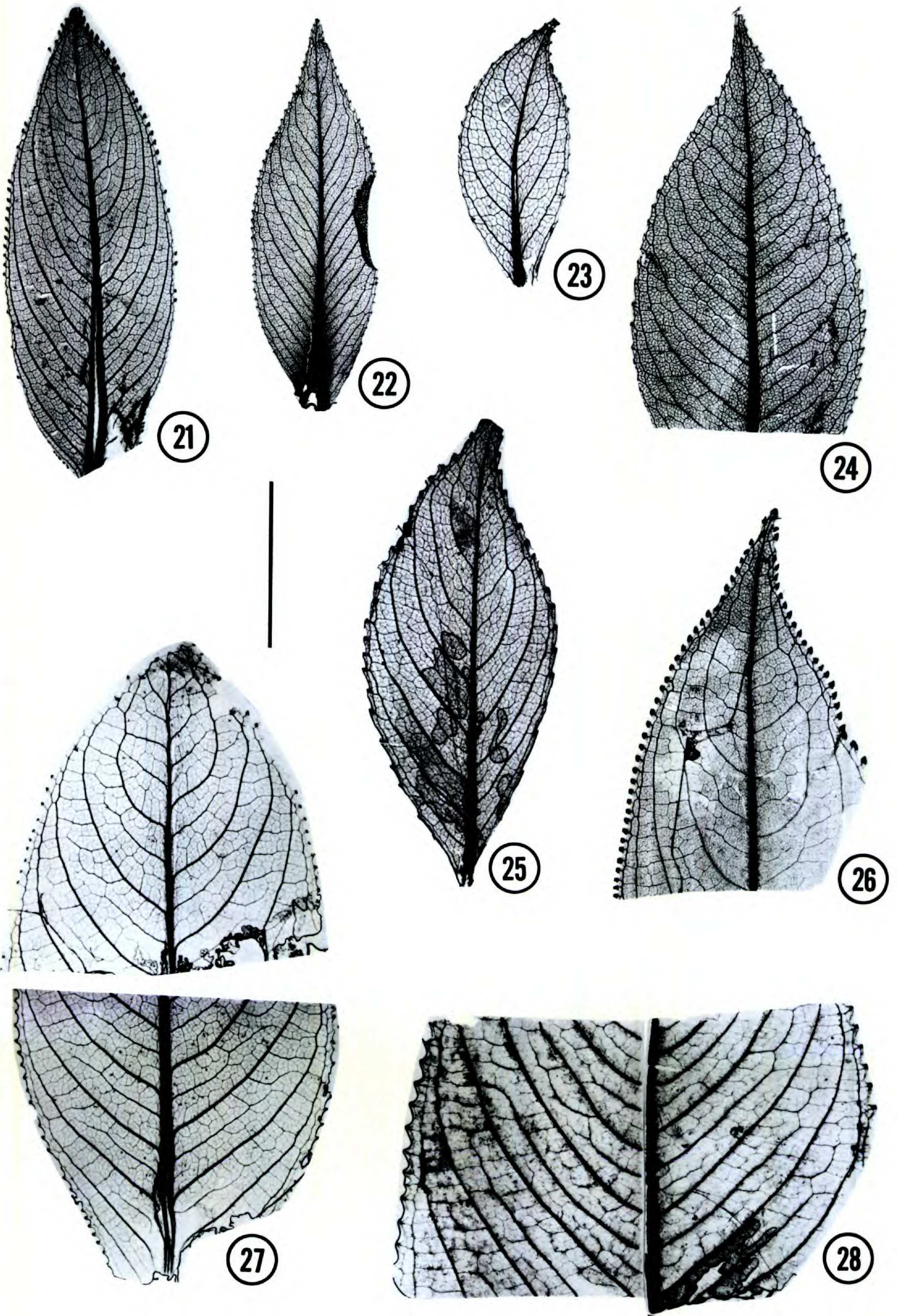
Interpretation of character state polarities begins with the analyses of Hickey & Wolfe (1975), Doyle & Hickey (1976), and Doyle (1978). Hickey and Wolfe derive most of their conclusions from comparisons of leaf clearings based on the approximately 20,000 specimens represented in the two major cleared leaf collections in the United States. Doyle's (1978) and Hickey & Doyle's (1977) reviews comment on the one stratigraphic sample that has been analyzed in detail for both pollen and leaf fossils, the Potomac formation of the eastern United States. From those works, it appears that the earliest known angiosperm leaves are simple, entire, pinnately veined, first rank forms, with several orders of anastomosing veins and freely ending veinlets. The earliest forms illustrated in those studies show a festooned brochidodromous secondary architecture of Hickey's (1979) system. Hickey & Taylor (1989) have refined this model using cladistic comparisons of primitive genera with suggested angiosperm sister groups and with Early Cretaceous angiosperm fossils. The "ancestral angiosperm leaf" is conjectured to have a sheathing base with 4–5 separate vascular bundles entering the petiole producing pinnate (brochidodromous) or palmate (palinactindromous) venation in ovate leaves. Chloranthoid teeth are found near the apex.

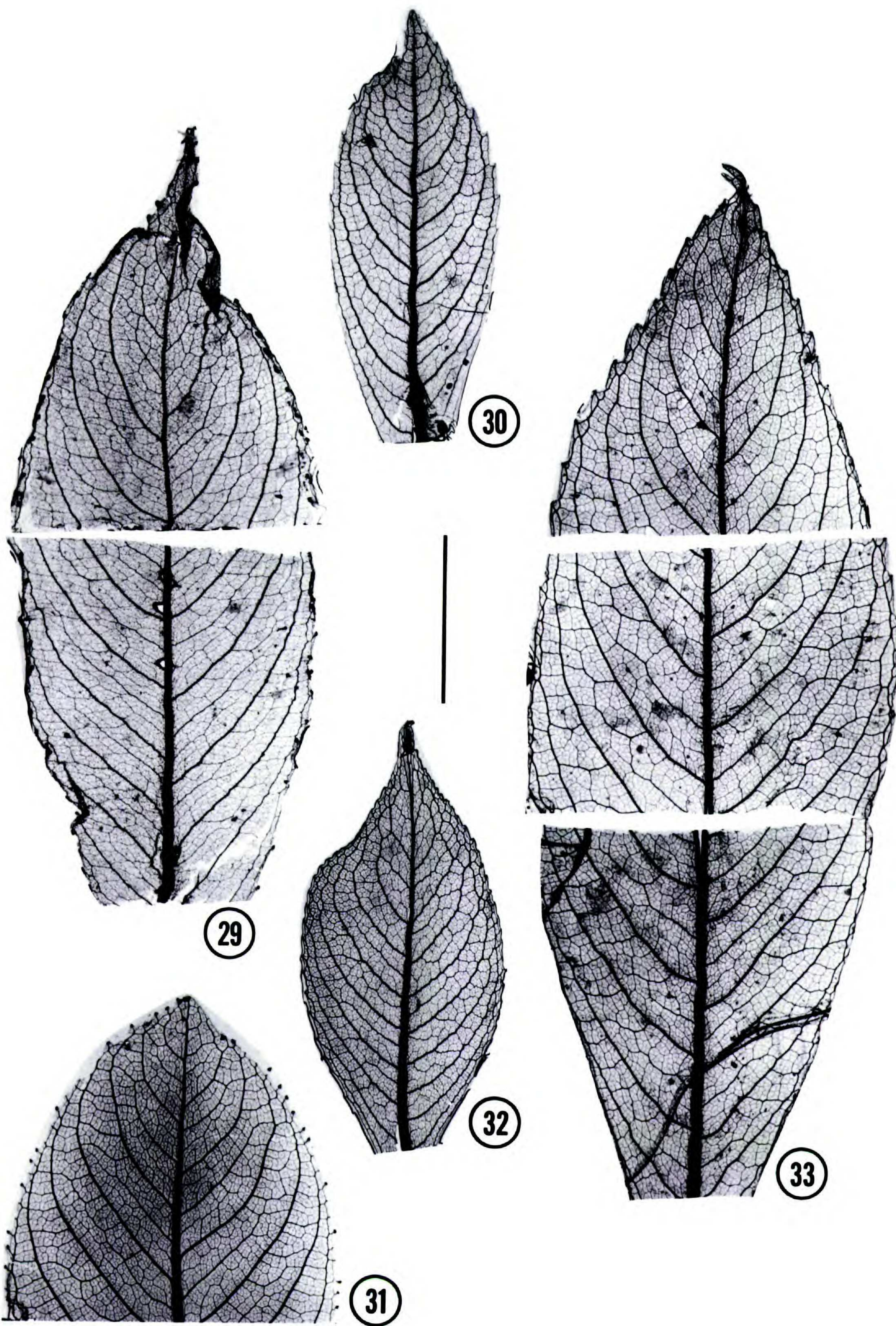
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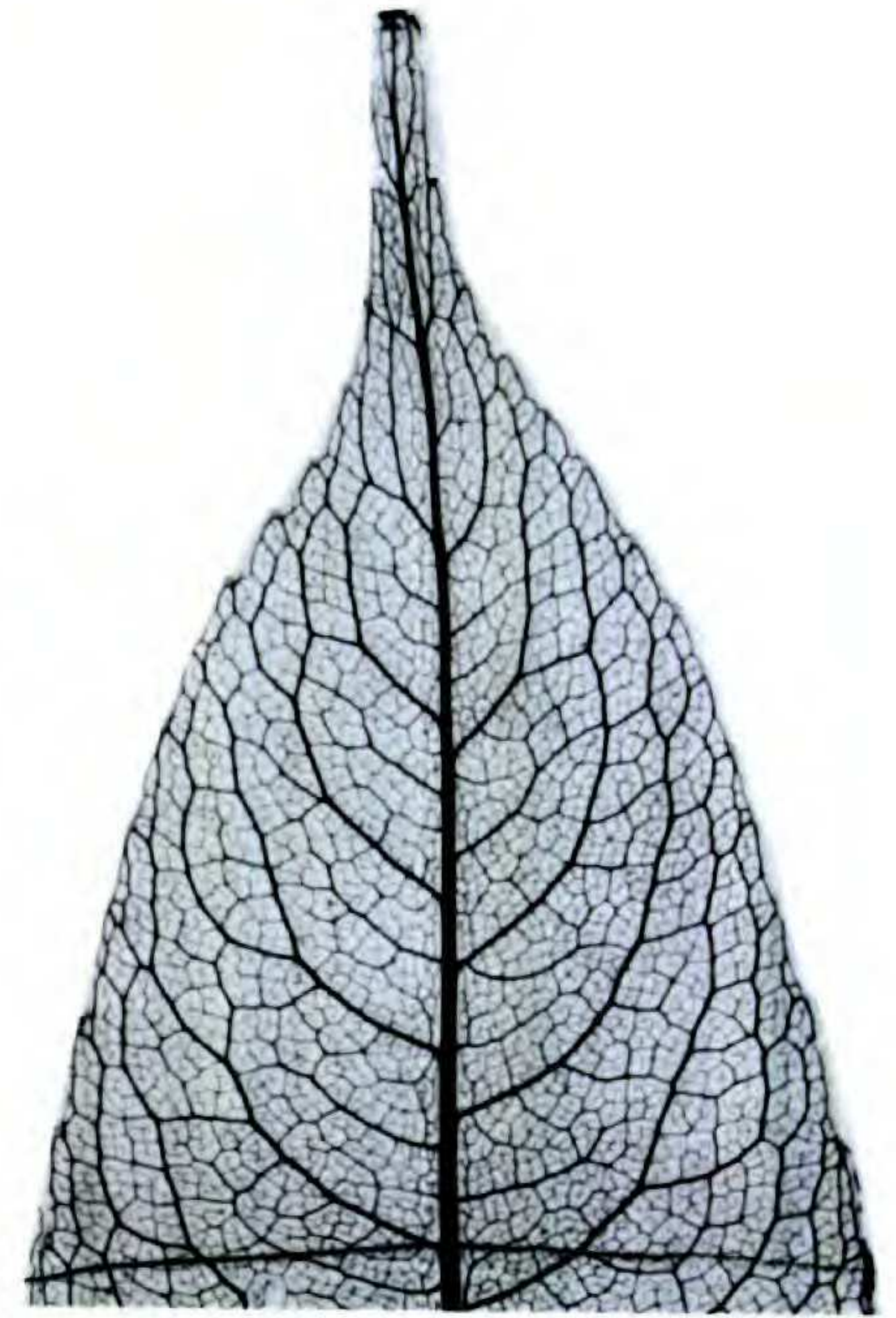
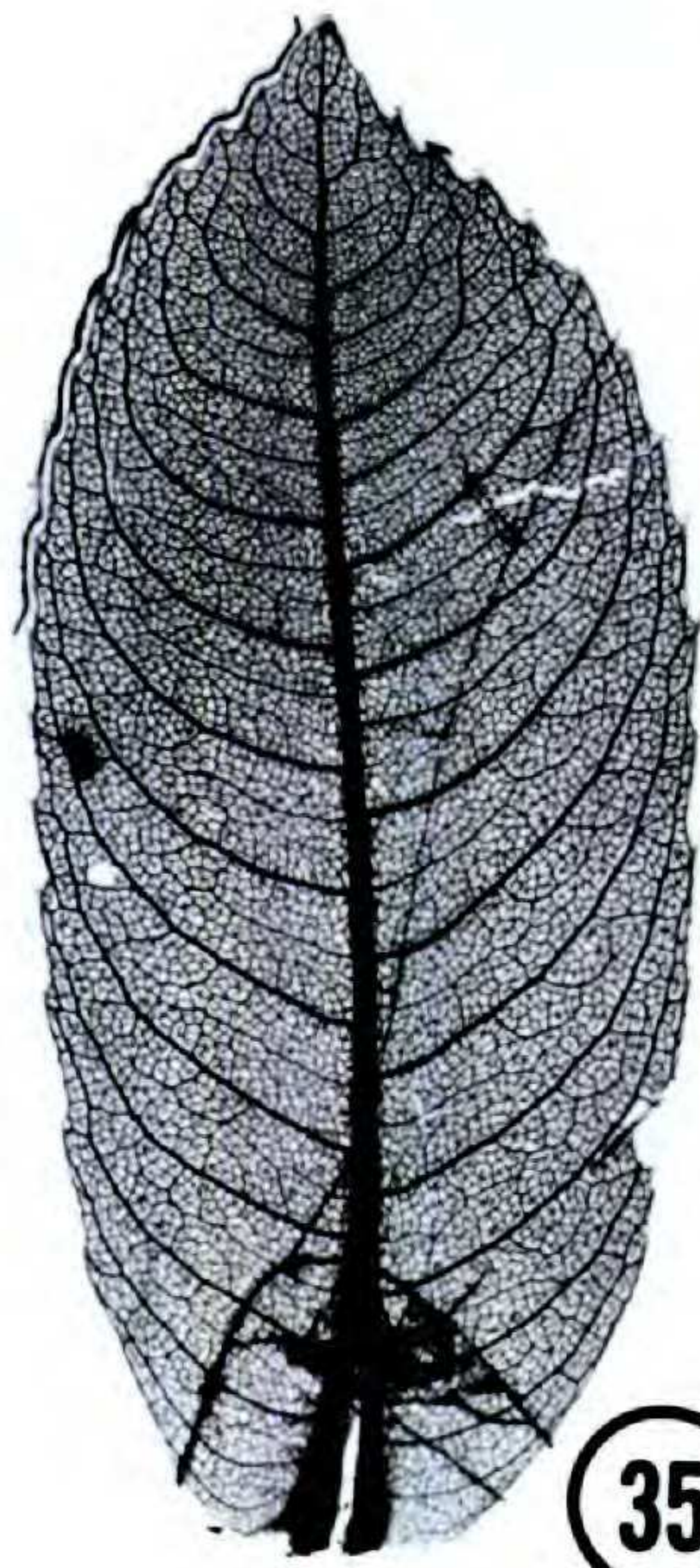
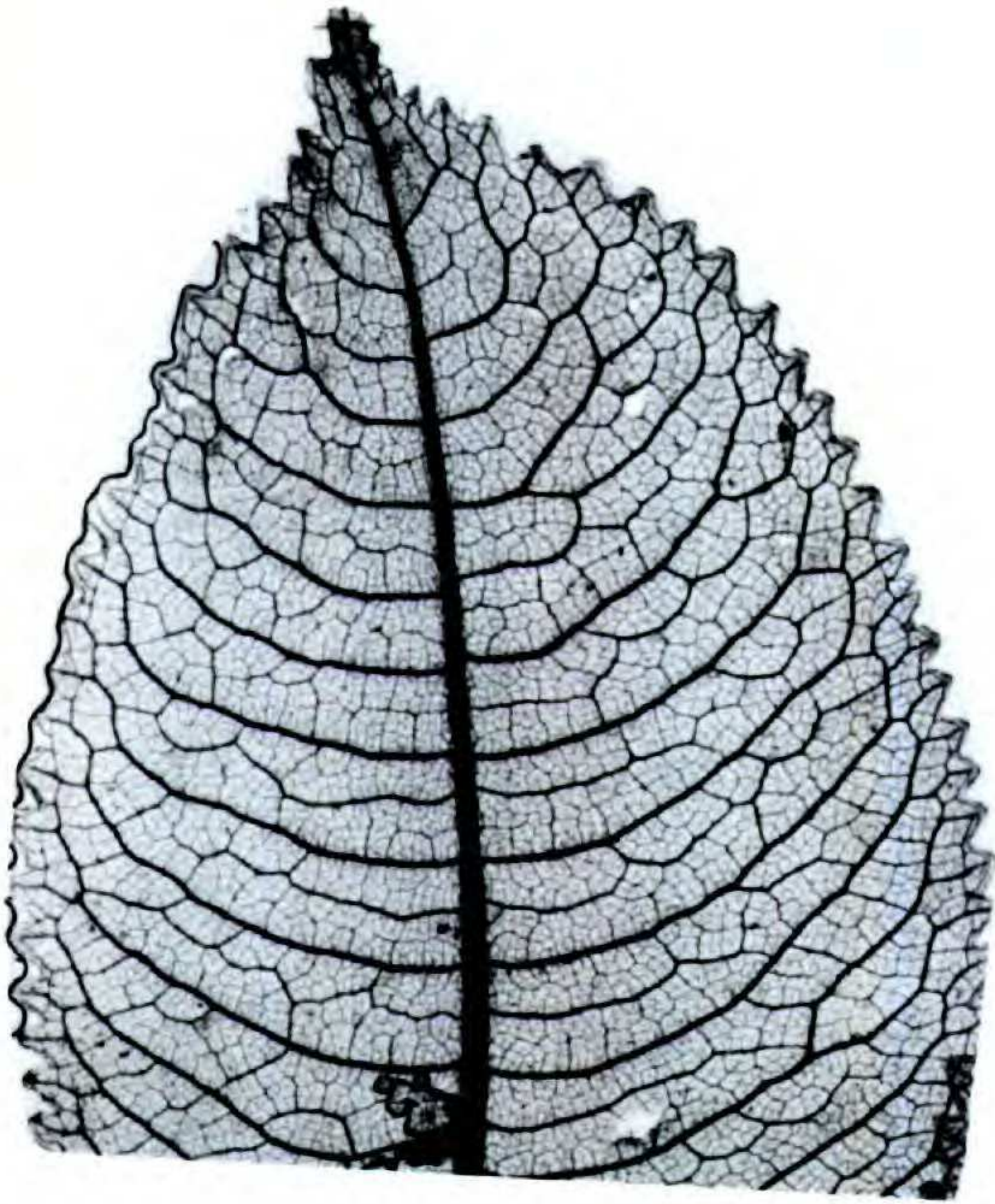
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FIGURES 21–28. Leaf clearings of *Hedyosmum*. —21. *H. goudotianum*. —22. *H. colombianum*. —23. *H. coreanum*. —24. *H. crenatum*. —25. *H. steinii*. —26. *H. spectabile*. —27. *H. anisodorum*. —28. *H. strigosum*. Scale line = 2 cm.

FIGURES 29–33. Leaf clearings of *Hedyosmum*. —29. *H. scaberrimum*. —30. *H. dombeyanum*. —31. *H. translucidum*. —32. *H. lechleri*. —33. *H. sprucei*. Scale line = 2 cm.

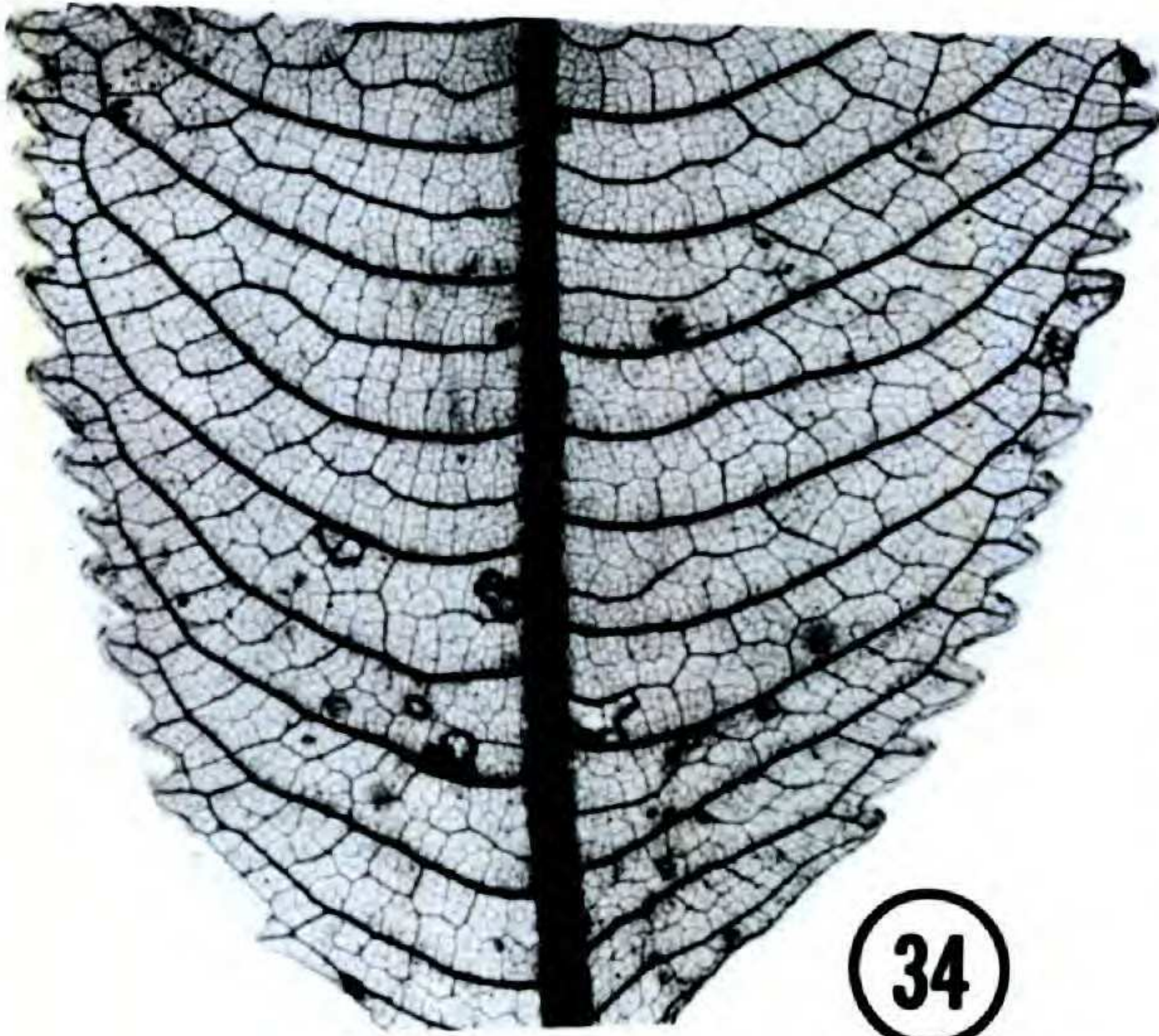
FIGURES 34–40. Leaf clearings of *Hedyosmum*. —34. *H. scabrum*. —35. *H. parvifolium*. —36. *H. cumbalense*. —37. *H. angustifolium*. —38. *H. cuatrecazanum*. —39. *H. peruvianum*. —40. *H. luteynii*. Scale line = 2 cm.







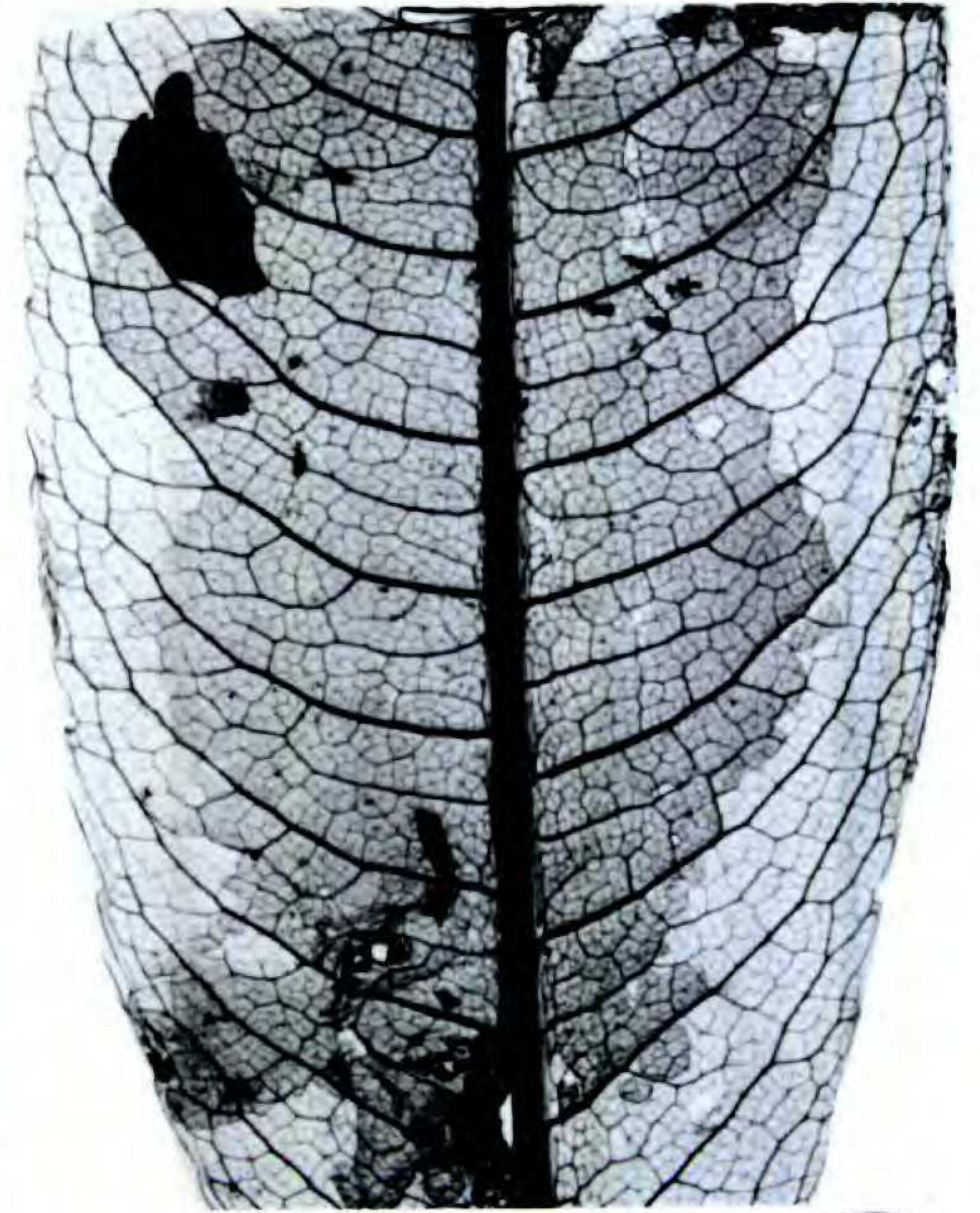
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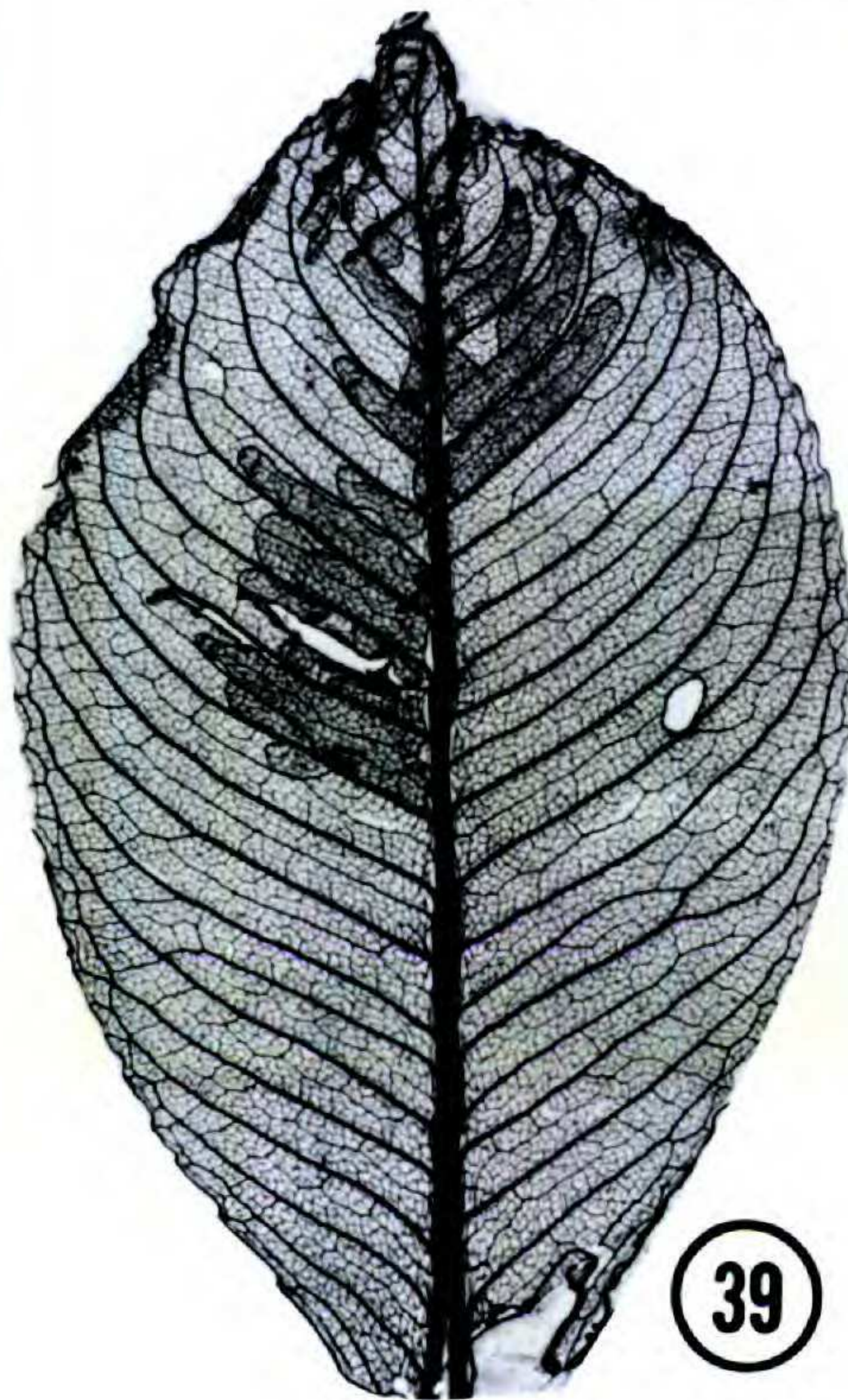
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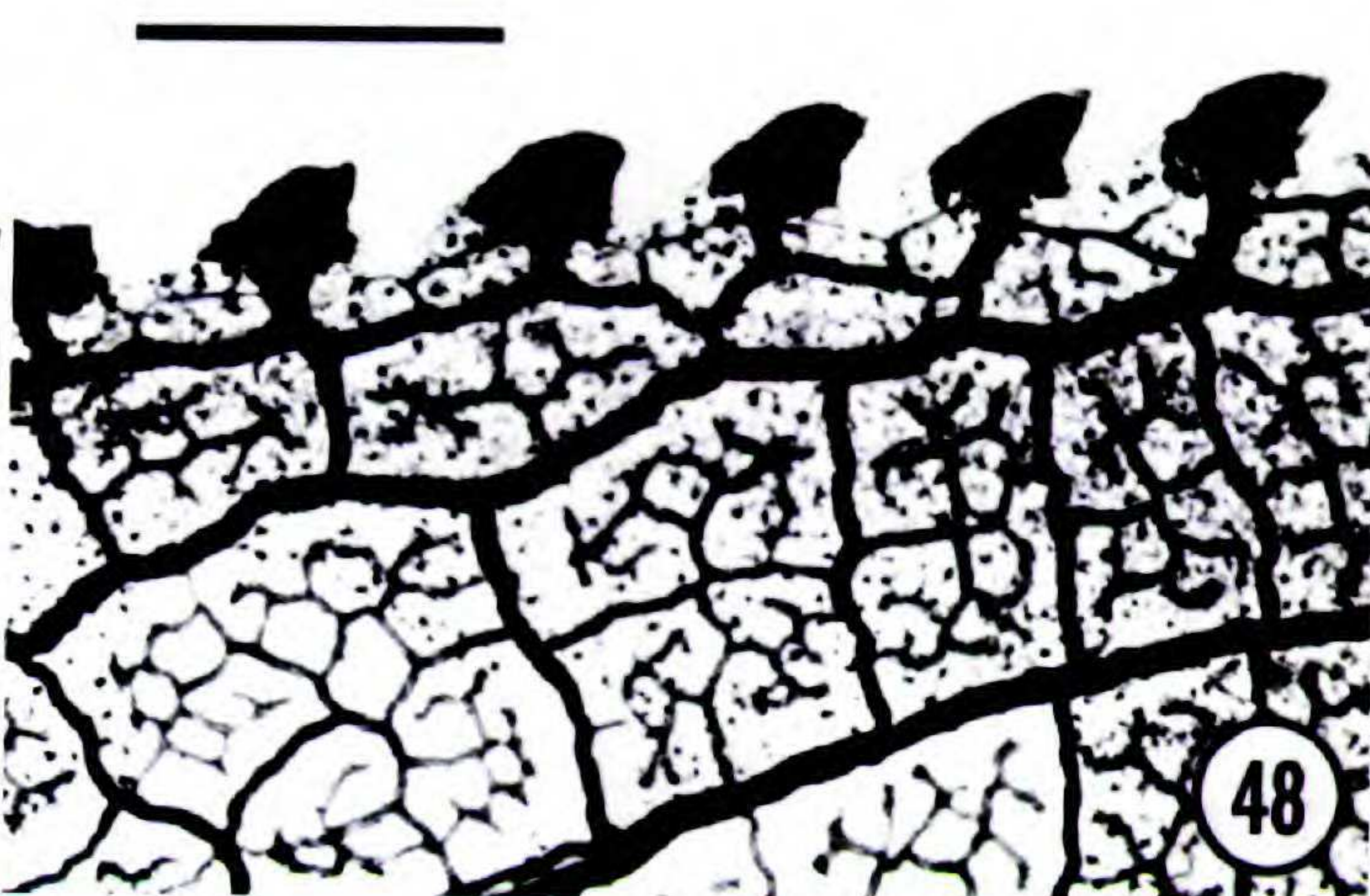
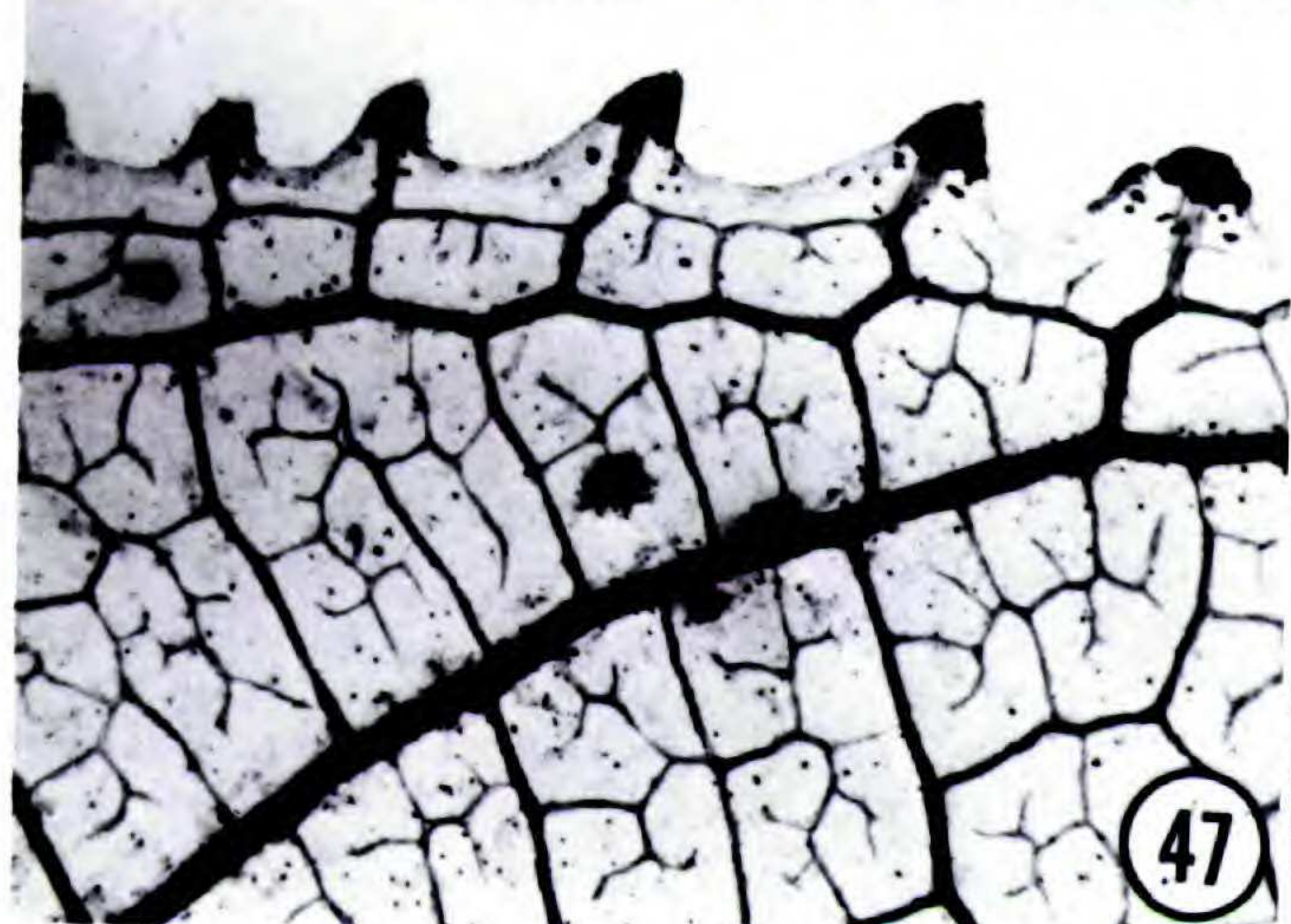
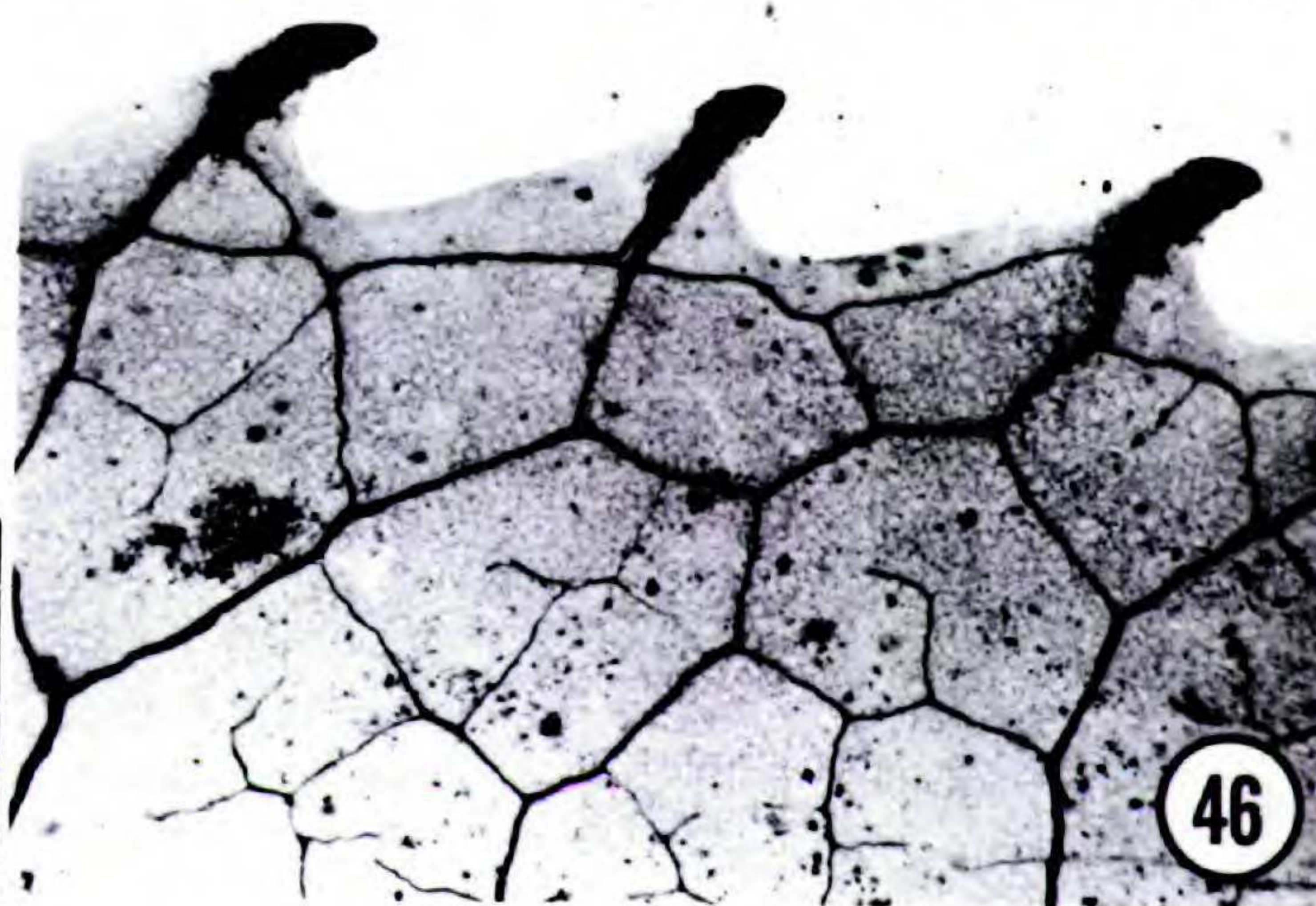
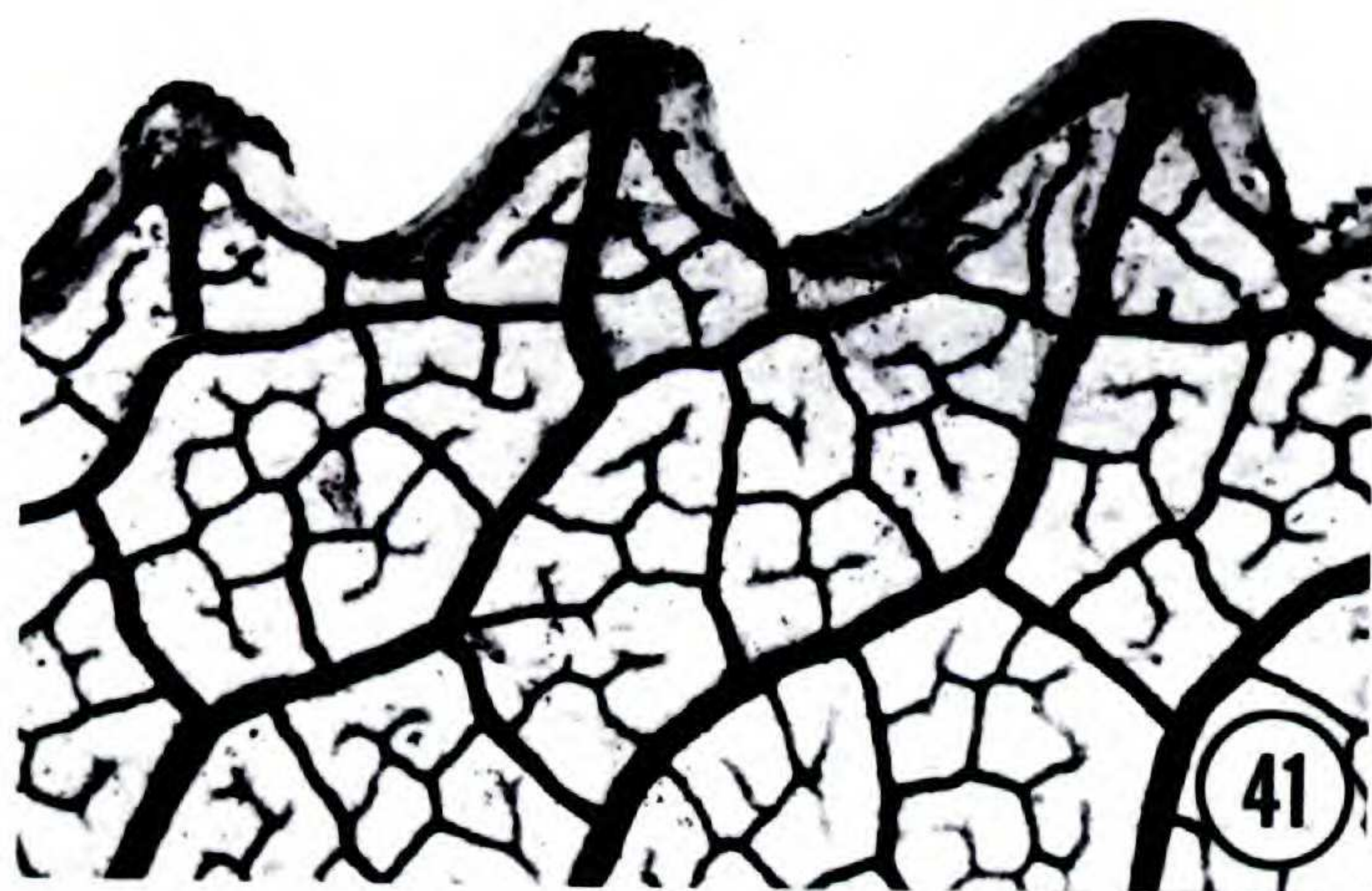
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closely to these early leaves, the secondary veins tend to be widely spaced, are never narrowly spaced, and form irregularly shaped intercostal areas. Beyond this observation, there is no established polarity regarding the spacing of secondaries. Possible ranalian outgroups give conflicting evidence. Leaves with few, widely spaced secondaries occur in the Amborellaceae and Austrobaileyaceae while leaves with numerous, closely spaced secondaries are found in Trimeniaceae, Winteraceae, Degeneriaceae, and Eupomatiaceae (G. Upchurch, pers. comm.).

Transitional secondary venation patterns are common and there is too little comparative information to polarize the character states with confidence. Prominent secondary arches occur and often tertiary and higher order loops form between the secondary arches and the margin (e.g., *Sarcandra glabra* (Figs. 1, 2), *Ascarina lucida* (Fig. 3), and *A. rubricaulis* (Fig. 6)). Higher rank leaves have a higher number of secondaries, and brochidodromy tends toward eucamptodromy at the proximal end of the leaf (e.g., *Hedyosmum grisebachii* (Fig. 10), *H. costaricense* (Fig. 16), *H. racemosum* (Fig. 17), *H. mexicanum* (Fig. 19), *H. bonplandianum* (Fig. 20)).

The semicraspedodromous pattern is seen where the tooth vein originates prominently from secondary arches of the brochidodromous plan as seen in *Sarcandra glabra* (Figs. 1, 2), *Ascarina philippinensis* (Fig. 4), *Chloranthus spicatus* (Fig. 5), and *Hedyosmum nutans* (Fig. 9). In Hickey & Wolfe's (1975) taxonomic review, semicraspedodromous leaves show up for the first time in the dilleniid genera, a group parallel to and slightly higher than the magnoliids. We have seen no previous discussion relating this pattern closely to the brochidodromous leaves and yet it is found among genera in the Chloranthaceae that on other grounds are more primitive than *Hedyosmum*. Lorence (1985) included a survey of the leaf architecture in his monograph of the relict genera of the Monimiaceae of the Malagasy region. The patterns illustrated are mostly brochidodromous but include admixtures of craspedodromous patterns in *Ehippiandra madagarcariensis* and *Tambourissa ficus*, and semicraspedodromous in *E. tsaratanensis* and *T. trichophylla*. It appears to us that the developmental and phylogenetic relationships

between brochidodromous and semicraspedodromous leaves are quite close and need to be adequately analyzed. Existing concepts should be regarded as tentative at this point but we suggest that the semicraspedodromous leaf type is one of, if not the earliest, associated with toothed leaves. The fact that many early ranalian leaves are entire-margined may have helped to obscure this relationship.

Fully eucamptodromous leaves can be seen in *H. goudotianum* (Fig. 21), *H. steinii* (Fig. 25), and *H. anisodorum* (Fig. 27). Some forms of eucamptodromous leaves (e.g., *H. gentryi* (Fig. 11), *H. neblinae* (Fig. 13), *H. arborescens* (Fig. 15)) have secondary arches tending to become straightened into an intramarginal vein. Without direct evidence, but because of the common association of brochidodromous and eucamptodromous venation patterns, we hypothesize that eucamptodromy is derived from an earlier brochidodromous prototype through a shift in ontogeny.

The large majority of leaves in this family are elliptic (narrowly elliptic with a length/width ratio of 4.3:1 to widely elliptic with a length/width ratio of 1.4:1). Leaves may be ovate (Fig. 1, *Sarcandra glabra*) or obovate (*Hedyosmum cuatrecazanum* (Fig. 38) and *H. peruvianum* (Fig. 39)). In most cases the tip is acuminate and the base cuneate or decurrent. Leaf size ranges from 10 to 300 mm and length and width seem tightly correlated as seen in Figure 49.

In the scatter plots (Fig. 49), the largest leaves (*Hedyosmum sprucei*, *H. anisodorum*, *H. strigosum*, *H. pungens*, *H. peruvianum*) occur in low to mid elevations in the Andes and Central America, whereas species with the smallest leaves (*H. dominicense*, *H. pseudoandromeda*, *H. burgerianum*, *H. cumbalense*) are found on exposed ridgetops or high elevations. Species with leaves representing the central values of the scatter plots have a variety of habitat preferences that show no ready correlation.

Teeth in this family had been referred to by Hickey & Wolfe (1975) as chloranthoid, and Hickey & Taylor (1989) regard that type as prototypical for the angiosperms. However, we have noted that the leaf teeth in this family are quite variable and difficult to ascribe to one familial type (see

←
FIGURES 41–48. Leaf tooth types. Cleared leaves of *Hedyosmum* and *Sarcandra*. —41. *H. scabrum*, type 1a.—42. *H. cumbalense*, type 1b.—43. *H. gentryi*, type 2a.—44. *H. arborescens*, type 2b.—45. *Sarcandra glabra* subsp. *glabra*, type 2b.—46. *S. glabra* subsp. *brachystachys*, type 2c.—47. *H. anisodorum*, type 3.—48. *H. spectabile*, type 3. Scale line = 2 mm.

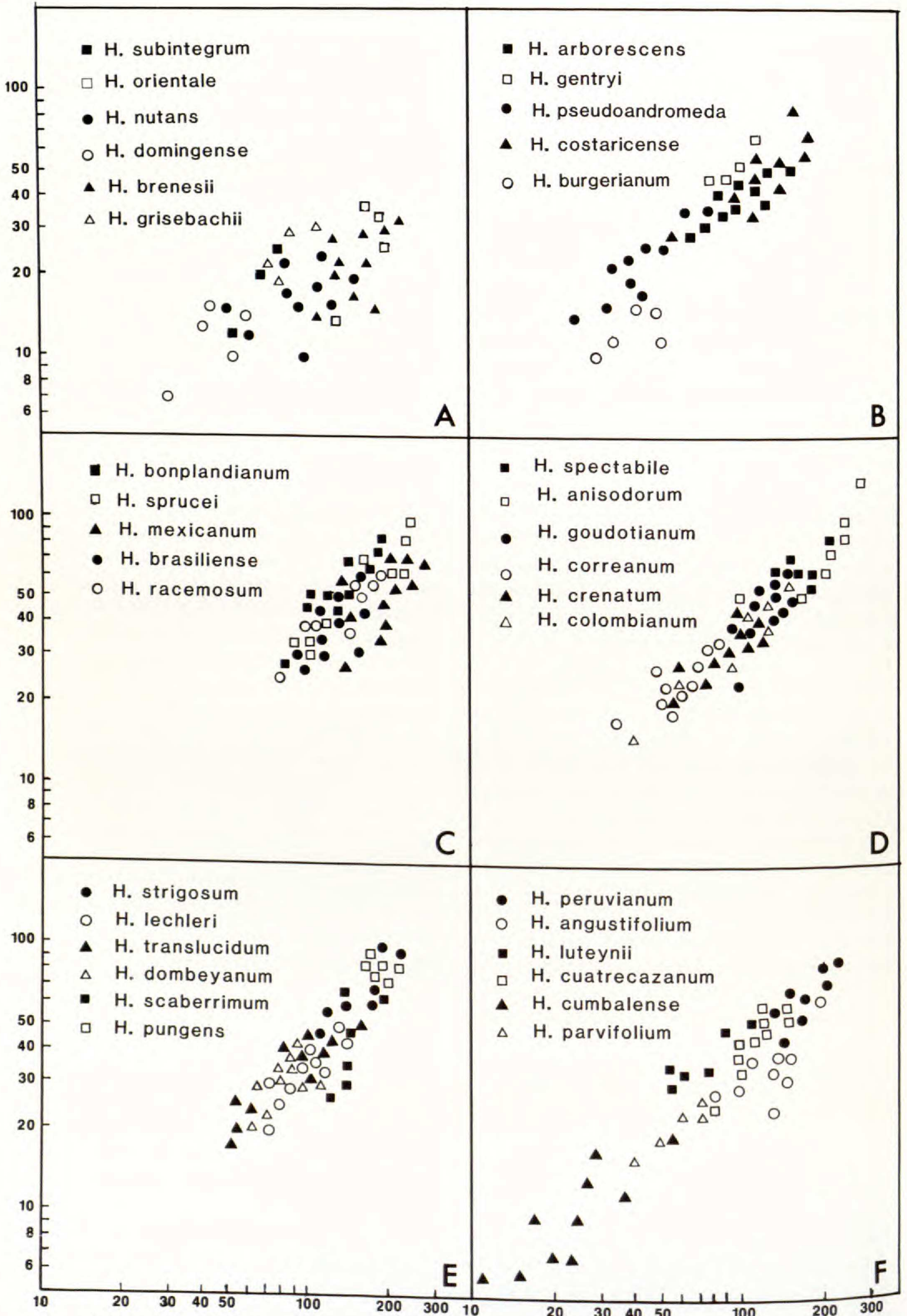


FIGURE 49. *Hedyosmum* leaf length (x axis) and width (y axis) in mm. Log scales. Up to ten specimens, when available, were used in each species sample.

Figs. 41–48). We categorized the leaf teeth of the Chloranthaceae as follows: type 1a (Fig. 41) is a broad tooth with a median vein usually arising from a secondary vein; it is symmetrically disposed between two smaller lateral and marginal converging veins. The three veins end in a vascular plexus distal to which appears a hydathodal glandular tip. On at least one specimen (*Chloranthus* sp.) a large stomate was noted on the surface of the tooth apex. Tooth type 1b (Fig. 42) still has the symmetrically converging lateral veins, but the tooth itself is shallow with only a small glandular tip protruding. Teeth of several species (*Hedyosmum grisebachii*, *H. subintegrum*, *H. nutans*, and *H. sprucei*) are not clearly placed into either type 1a or type 1b and are therefore coded simply as type 1 (Table 2). All the remaining teeth tend to have tips strongly curved toward the distal end of the leaf. The tooth apex is often oriented very close to the distal margin of the sinus. Type 2a (Fig. 43) has the median vascular bundle fused some distance back from the apex of the vascular plexus to the exmedial marginal vein. The admedial lateral becomes a marginal vein following around the sinus. The admedial lateral enters the tooth near the tip of the vascular plexus. In type 2b (Figs. 44, 45) the medial vein and the exmedial vein are fused far back from the tooth apex, and the admedial lateral follows the same path as the previous type. The unique feature is that the vascular plexus extends a greater distance into the attenuate leaf tooth. In type 2c (Fig. 46) the medial vein enters into the tooth with one small lateral vein merging far back from the tooth tip. The pattern is variable. There can be admedial, exmedial, or no lateral veins converging. Type 3 teeth (Figs. 47, 48) have a prominent densely sclerotic tip. They are vascularized by a prominent median vein with 0 to 2 converging lateral veins well inside the leaf margin. The nature of the teeth is currently being examined histologically. It is unclear at this point as to what exactly characterizes a chloranthoid tooth, if in fact, such a generalization can be made.

Since data are available for 37 of the 40 species of *Hedyosmum*, relationships within that genus can be discussed in greater detail. Specific architectural features support Todzia's (1988) classification, which recognizes two subgenera and five sections (Table 1). Leaves within subg. *Hedyosmum* all are lanceolate to narrowly elliptic with length/width ratios ranging from 10:1 to 3.3:1. Leaves in the 31 species of subg. *Tafalla* represented in our sample are mostly elliptic, with only a few species having obovate or lanceolate leaves. The length/width ratios of subg. *Tafalla* range mostly from

1.7 to 3.3:1 with a few exceptions (*H. brasiliense*, 3.6:1; *H. mexicanum*, 3.9:1; *H. scaberrimum*, 3.9:1; *H. angustifolium*, 4.1:1).

The median leaf rank differs among sections of the two subgenera presently recognized in *Hedyosmum*. Section *Oriente* and sect. *Hedyosmum* of subgenus *Hedyosmum* have median leaf ranks of $2r^1$ and $2r^{1.5}$ respectively, while sects. *Microcarpa*, *Macrocarpa*, and *Artocarpoides* of subg. *Tafalla* have higher median leaf rank ($2r^2$, $2r^3$, $2r^3$ respectively). Within sect. *Oriente* the species with the lowest leaf rank order, *H. orientale* ($2r^0$), is clearly the most primitive species in that group. This agrees with Hickey & Taylor's (1989) description of early angiosperm leaves that have very low rank. Within each section of *Hedyosmum*, however, leaf rank varies widely among species. Although the phylogeny within sect. *Microcarpa* is still in question (Todzia, 1988), rank may be indicative of species relationships. For example, the following species pairs are more closely related to each other than to other species within sect. *Microcarpa*, and each pair possesses the same leaf rank: *H. gentryi* and *H. neblinae* ($2r^3$); *H. costaricense* and *H. burgerianum* ($2r^2$); *H. racemosum* and *H. sprucei* ($3r^1$); *H. correanum* and *H. colombianum* ($2r^1$); and *H. goudotianum* and *H. spectabile* ($4r^0$).

Within *Hedyosmum* all tooth types are present except for type 2C. Section *Microcarpa* has the most varied array, including 1A, 1B, 2A, 2B, and 3. Species with type 3 teeth (*H. goudotianum*, *H. correanum*, *H. anisodorum*, *H. steinii*, *H. spectabile*, *H. scaberrimum*, and *H. translucidum*) appear quite closely related. *Hedyosmum burgerianum* and *H. costaricense* appear to be closely related by virtue of their widely spaced teeth. Considering its size, sect. *Macrocarpa* has the most limited range of all the groups with types 1A and 1B predominant and only one instance of type 2A, in *H. parvifolium*. In subg. *Hedyosmum*, sect. *Hedyosmum* and sect. *Oriente* have 1A, 1B, 2A, and 2B type teeth.

An intramarginal vein is present in only a few species, *H. pseudoandromeda* (Fig. 12), *H. gentryi* (Fig. 11), *H. neblinae* (Fig. 13), *H. arborescens* (Fig. 15), and *H. costaricense* (Fig. 16), and appears to be one of the defining characters of this group within the large sect. *Microcarpa*. Within sect. *Macrocarpa* distance between secondary veins appears to be a useful character. Closely spaced secondaries are present in *H. parvifolium* (Fig. 35), *H. cumbalense* (Fig. 36), *H. cuatrecazanum* (Fig. 38), *H. peruvianum* (Fig. 39), and *H. luteynii* (Fig. 40). These species are more closely related

to each other than to *H. angustifolium* (Fig. 37) and *H. scabrum* (Fig. 34) which, in addition to having more widely spaced secondary veins, also have a different pistillate inflorescence morphology.

Within *Hedyosmum* leaf architectural data do not appear to be correlated with elevation.

INTERGENERIC RELATIONSHIPS

Sarcandra, *Ascarina*, and *Chloranthus* all appear to have less well organized leaves than *Hedyosmum*. *Sarcandra* and *Chloranthus* leaves have widely spaced secondaries with poorly organized loops and unpredictable eucamptodromous patterns. *Ascarina lucida* has a primitive looping pattern and semicraspedodromous tooth vascularization. The teeth of leaves of all three genera are well vascularized.

There is some resemblance between these three genera and *Hedyosmum subintegrum* and *H. brasiliense*. *Hedyosmum brasiliense* in particular has anastomosing tertiaries. That is, the exmedial tertiary of the distal secondary fuses with the admedial tertiary of the next most basal secondary to form a craspedodromous vein that follows the course of other secondaries toward the margin.

In general, all *Hedyosmum* species examined have well-organized secondaries, good areolation, high leaf rank, reduced teeth, and close secondary spacing. It is the only genus that has developed intramarginal veins and specialized crystal patterns.

All four genera have teeth within the same size range and vascularization having the same brochidodromous/eucamptodromous series. All leaves have generally decurrent basal laminae, acute to acuminate tips, and tertiaries that seldom form predictable patterns.

INTERFAMILIAL RELATIONSHIPS

Little detailed information on leaf architecture of other ranalian families is available, but we do have a well-illustrated guide to the Lauraceae (Klucking, 1987) and the Annonaceae (Klucking, 1986). Lorence (1985) illustrated leaf clearings of species of Monimiaceae from the Madagascar region. An analysis of these works shows a number of similarities with the Chloranthaceae and a number of features that emphasize their lack of a close relationship.

The Lauraceae generally resemble the Chloranthaceae in having decurrent leaf bases, attenuate leaf tips, ovate leaf shape, and irregularly spaced secondary veins. Other resemblances are found

among only some genera, and often only in certain species of these genera. These similarities include irregularly spaced, looped brochidodromous secondaries (*Licaria*, *Litsea*, *Aiouea*, *Aniba*); variable spacing and frequency of secondaries (*Nectandra*, *Ocotea*); forked secondaries (*Beilschmiedia*); eucamptodromous secondaries (*Cryptocarya*); and tendencies toward intramarginal veins (*Nothophoebe*, *Ocotea*).

Major differences from the Chloranthaceae include entire margins in all lauraceous genera, the presence of lateral primary veins in some species, the presence of often orthogonal tertiaries, a strong tendency toward percurrent tertiaries (*Actinoraphe*, *Alseodaphne*, *Beilschmiedia*, *Cinnamomum*, *Cryptocarya*, *Litsea*, *Mezilaurus*, and *Nectandra*). Admedial vein endings of several orders are found in *Beilschmiedia*. Ascending acrodromous secondaries are found in *Cinnamomum*, *Cryptocarya*, *Lindera*, *Neocinnamomum*, and *Neolitsea*. The synapomorphies found in the Lauraceae indicate an ancient separation between the two families.

While most phylogeneticists classify the Trimeniaceae with the Lauraceae, away from the Piperales (Cronquist, 1981; Takhtajan, 1987), Endress (1987) has called attention to numerous similarities between the Chloranthaceae and their proposed closest relatives, the Trimeniaceae. We compared specimens of *Trimenia* from the herbarium of the Missouri Botanical Garden, but specimens of *Piptocalyx* were not available. *Trimenia neocaledonica* Baker f. from New Caledonia has an entire-margined elliptic leaf of first leaf rank with a well-developed intramarginal vein. Secondary veins, averaging nine on each side of the midrib, are often branched, giving the secondaries a cladodromous appearance. This leaf shows little resemblance to any we examined in the Chloranthaceae. *Trimenia papuana* Ridl. from Papua, New Guinea, has a toothed elliptic leaf with about 28, often bifid secondaries per side. They are regular in arrangement, and therefore at least second rank order, with one intersecondary usually found per intercostal area. The secondaries end short of the margin at an undulating intramarginal vein, which follows the outline of the tooth lobes and shallow sinuses. Veins leave the intramarginal vein in a semicraspedodromous pattern and appeared to run to the base of the sinuses just distal to the tooth. The tooth has a glandular apiculus not characteristic of any seen in the Chloranthaceae. *Trimenia* tooth architecture of our specimens does not seem to fit any of the chloranthoid types that we have identified. However, Endress (1987, fig. 191) illustrated a cleared

tooth of the *T. papuana*, which we would interpret as similar to our type 3 chloranthoid type.

The opposite phyllotaxy and leaf base morphology of *Trimenia* are suggestive of the Chloranthaceae, and in both families tooth vascularization always seems to arise from brochidodromous loops or collectors and never from secondaries directly. In other ways they are quite distinguishable. In the Chloranthaceae, the main tooth vascularization is always direct and never by way of the sinus. No eucamptodromous or brochidodromous patterns were found in the *Trimenia* specimens examined.

In our limited observations of *Trimenia*, its leaves appear to have specialized independently and to a somewhat higher level than most Chloranthaceae. However, the postulated close relationship is not negated by our evidence.

Lorence's (1985) study of the Malagasy Monimiaceae reveals characters in those Lauralian genera that closely resemble characters found in the leaves of Chloranthaceae. Second rank, festooned brochidodromous leaves are found in *Monimia* and *Decaryodendron* with eucamptodromy found in *M. ovalifolia*. Widely spaced secondaries in craspedodromous or semicraspedodromous leaves are found in *Ehippiandra* and *Tambourissa*. Margins range from entire to dentate in the family. Dentate leaves are noted in *Hortenia* and *Tambourissa* but they have monimiod vascularization. That type does not resemble the Chloranthaceae in that the median vein servicing a tooth supports loops on both sides, which decrease in size toward the margin and tooth apex. In *Tambourissa*, species with entire adult leaves have dentate juvenile leaves. However close the two families are later judged to be, it is clear that they share the same grade or level of specialization of leaf architecture.

Klucking (1986) studied an extensive sample of the Annonaceae, which allows a detailed comparison with the Chloranthaceae. Again, it appears that the differences mitigate against postulating a close relationship.

Similarities between the Chloranthaceae and the Annonaceae include an ovate to elliptic shape and usually eucamptodromous venation. Brochidodromous leaves are found in a few genera (*Mezozettia*, *Artabotrys*, and *Marsypopetalum*) but not commonly. Decurrent secondaries are found only in *Cleistopholis*. Attenuate leaf tips are common in most genera.

A few species from Klucking's illustrated Annonaceae sample bear a close resemblance to *Sarcandra* and have a generally low rank. These include *Annona reticulata* L., *Guatteria schomburgkiana* C. Martius, *Desmopsis mexicana* R. E. Fries,

Greenwayodendron suaveolens Engl. & Diels, *Goniothalamus repevensis* Pierre, *Porcelia macrocarpa* (Warm.) Fries, *P. nitidifolia* Ruiz Lopez & Pavón, *Sageraea glabra* Merr., *Polyalthia subcordata* Blume, and *Oxandra riedeliana* R. E. Fries. These specimens do not come from geographically close localities but rather from the tropical range of the Annonaceae.

All of the specializations found in the Annonaceae represent trends not present in the Chloranthaceae. Among these are strongly percurrent tertiaries in most genera, the absence of teeth in all genera, close and regularly spaced secondaries, basal lamina insertion that is emarginate, blunt, incipiently cordate in species of *Friesodielsia*, *Dasydaschalon*, and *Ellipeia*; strongly ascending secondaries in *Platymitra*, *Mitrephora*, and *Kings-tonia*, obovate shape in *Asimina*, and emarginate leaf tips in *Goniothalamus*.

Many more studies need to be made of ranalian families, especially among the genera having low rank leaves. Important early dicot trends are abundant among ranalian genera, but we have little understanding of the systematic significance of their leaf architecture.

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